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A MATHEMATICAL MODEL OF A PREDATOR-PREY SYSTEM WITH PERIODIC CARRYING CAPACITY

by

© Luis Mañetto

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graudate Studies and Research, for acceptance, a thesis entitled A MATHEMATICAL MODEL OF A PREDATOR-PREY SYSTEM WITH PERIODIC CARRYING CAPACITY submitted by Luis Mañetto in partial fulfilment of the requirements for the degree of Master of Science.

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ABSTRACT

We deal with a model of predator-prey interactions where the effect of the environment on the prey species is assumed to undergo periodic fluctuations. Since, in a biological setting, it is most desirable that both predator and prey populations achieve a stable state of equilibrium, we are interested in finding conditions on the parameters for this to be so.

We first look at solutions for the unperturbed model, i.e. when the influence of the environment is independent of time, and then consider solutions when a small, time-dependent, perturbation is introduced with a view to investigating the existence of a stable limit cycle.

In Chapter II we attempt to find conditions on g, p and K for there to exist a small amplitude perturbed periodic solution instead of the equilibrium, and such that this solution tends towards the equilibrium as $\varepsilon \to 0$. We are also interested in seeing if the stability conditions are preserved, i.e. if a stable (unstable) periodic solution corresponds to a stable (unstable) equilibrium.

In Chapter III we look at the case when the equilibrium corresponding to the autonomous system is unstable and consider conditions for there to exist a perturbed stable limit cycle for the nonautonomous system.

In order to carry out the analysis we use perturbation techniques and the Implicit Function Theorem, referring to Freedman [4].

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CHAPTER I

1.1. Background. The classical model for a predator-prey system with continuous growth is that of Lotka (1925) and Volterra (1926)

$$x'(t) = x(t)[a - \alpha y(t)]$$

$$y'(t) = y(t)[-b + \beta x(t)].$$

Here $x(t)$, $y(t)$ are the populations (or densities) of prey and predator respectively, at time t. The parameter a is the birth rate of the prey, b the death rate of the predator, and α, β refer to the interactions between the species: all are positive numbers. These equations constitute the simplest representation of the essentials of a nonlinear predator-prey interaction (see May [15] and Maynard Smith [16]).

We consider a more general predator-prey model

$$x' = xg\big(x, K(t)\big) - yp(x) \tag{1.1a}$$

$$y' = y[-s + cp(x)] \quad c,s > 0. \tag{1.1b}$$

Here $K(t)$ is the carrying capacity, which refers to the equilibrium density attained by the prey in the absence of predation; it is obviously positive and is normally assumed to be periodic to account for seasonal effects of weather, mating habits, food supply, hunting or harvesting seasons, etc. $g\big(x, K(t)\big)$ is the specific growth rate of the prey in the absence of predators; we assume the behaviour of g to be determined by logistic growth, so that

$$g(0,K(t)) > 0, \quad g_x(x,K(t)) \leq 0 \text{ for } x \geq 0 \text{ and } g(K(t),K(t)) = 0.$$

These assumptions seem reasonable since one would expect the growth rate x' of the prey to increase for small x (when food provided by the environment is plentiful); as x increases one would expect the specific growth rate g to decrease owing to interaction between the species.

The predator response function $p(x)$ measures the rate at which prey are taken by a predator as a function of prey density x. In some models $p(x)$ is assumed to be unbounded above, as in the Lotka-Volterra model (see May [15]). In many models $p(x)$ is assumed bounded above (see Holling [11]). In some cases it is assumed that $p(x)$ has no concavity (as in Lotka-Volterra), or that it is always concave down, as in Holling [11]. There are models, however, in which $p(x)$ changes concavity: Haynes and Sisojevic [10] found experimental evidence for this. All these possibilities are incorporated in the following assumptions:

$$p(0) = 0, \quad p_x(x) > 0 \quad \text{for} \quad x \geq 0.$$

In the one-dimensional case

$$x' = xg(x,K(t)) \tag{1.2}$$

it can be shown that a stable solution of the equilibrium always exists. This is done by assuming that

$$m \leq K(t) \leq M, \quad x \geq 0$$

where m, M are positive constants. With the above assumptions on g we have $g(x,K(t)) > 0$ if $x(0) < m$, so that x is increasing. On the other hand, if $x(0) > M$ then $g(x,K(t)) < 0$ and x is decreasing.

Hence it is impossible for any solution $x(t)$ within $[m,M]$ to leave this interval and, by applying a theorem of Massera [14], we obtain a periodic solution of (1.2).

Cushing [2] analyses the model

$$x' = x\big(\alpha(t) - \lambda(t)x - \beta(t)y\big)$$

$$y' = y\big(-\gamma(t) + \delta(t)x - \mu(t)y\big)$$

where the coefficients α, β, γ, δ, λ, μ are periodic. By using bifurcation theory he is able to show that this system has a periodic solution provided the time average of the predator's death rate is in a suitable range. In [3] he extends his results to a system which models the interaction of n species under similar assumptions.

Freedman [5] considered system (1.1) with g independent of K and examined the stability of the equilibrium applying a graphical method of Rosenzweig and MacArther [17]. Freedman and Waltman [7],[8] investigated the classical two-dimensional Volterra predator-prey equations after a perturbation by functions of two variables: they give sufficient conditions for the perturbed system to have a limit cycle. In [8] they concentrate on the case where the first derivatives of the perturbation terms vanish at the critical point and the critical point remains fixed. They subsequently give conditions for the existence of a periodic solution and investigate the stability of such a solution.

1.2. <u>The model</u>. In this thesis we wish to consider system (1.1) under the assumption that

$$K(t) = K_0 + \varepsilon\kappa(t), \quad \kappa(t+\omega) = \kappa(t)$$

where K_0, ω are positive constants. Thus we have a periodically

fluctuating carrying capacity as against a constant one which has been treated in some papers (see e.g. [5]).

The usual assumptions on g, which generalise logistic growth, are:

$$g(0,K) > 0, \quad g(K,K) = 0, \quad g_x(x,K) \le 0,$$

$$g_K(x,K) \ge 0, \quad g_{xK}(x,K) \ge 0 \quad \text{for} \quad x \ge 0.$$

The assumptions for p have been stated in §1.1.

1.3. Equilibria of the unperturbed model. It follows from (1.1) that $(0,0)$ and $(K(t),0)$ are points of equilibrium for the system. However, since we are interested in an equilibrium interior to the first quadrant, we need to solve

$$-s + cp(x) = 0$$

and so we assume that $s/c \in$ Range $p(x)$.

Let $x = a$ be such that $p(a) = s/c$; then, using (1.1a), we put $b = ag(a,K(t))/p(a)$, and the required equilibrium point is denoted by (a,b).

To ensure that b is positive we need to assume $a < K(t)$ — otherwise extinction would occur.

1.4. Stability of the equilibrium. In order to examine the stability of this equilibrium we compute the variational matrix of system (1.1).

$$M(x,y) = \begin{pmatrix} g(x,K) + xg_x(x,K) - yp_x(x) & -p(x) \\ cy\, p_x(x) & -s + c\, p(x) \end{pmatrix}$$

So

$$M(a,b) = \begin{pmatrix} H(a,K) & -p(a) \\ bcp_x(a) & 0 \end{pmatrix}$$

where $H(a,K) = g(a,K) + ag_K(a,K) - bp_x(a)$. Since the product of the diagonal elements is zero and that of the off-diagonal elements is negative, the real parts of the eigenvalues of $M(a,b)$ have the same sign as $H(a,K)$. By a well-known theorem on stability (see [1], chap. 13) we arrive at the conditions

$H(a,K) < 0 \Rightarrow$ asymptotic stability

$H(a,K) > 0 \Rightarrow$ instability.

1.5. Phase plane of the unperturbed model. We consider now the motions in the first quadrant for system (1.1) for values of x such that $x = K_0$, $x > K_0$ and $x < K_0$. The slopes of the trajectories are given by

$$\frac{dy}{dx} = \frac{y[-s + cp(x)]}{xg(x,K_0) - yp(x)} \qquad (1.3)$$

Since $g(K_0,K_0) = 0$ we have

$$\left.\frac{dy}{dx}\right|_{x=K_0} = \frac{-s + cp(K_0)}{-p(K_0)} .$$

Now $p(K_0) > p(a) = s/c$ so that $\left.\frac{dy}{dx}\right|_{x=K_0} < 0$ and hence the solutions crossing the line $x = K_0$ do so with negative slope. Further, from (1.1a) $\left.x'\right|_{x=K_0} = -yp(K_0) < 0$, and so the solutions cross $x = K_0$ from right to left.

For $x > K_0$, $\frac{dy}{dx} = \frac{-s + cp(x)}{xg(x,K_0)/y - p(x)}$ and $xg(x,K_0)/y - p(x) < 0$ since $g(x,K_0) < 0$ for $x > K_0$. Also $p(x) > s/c$ for $x > K_0 > a$; hence, for fixed $x > K_0$,

$$\frac{-s + cp(x)}{-p(x)} < \frac{dy}{dx} < 0.$$

From (1.1a), $x'\Big|_{x>K_0} = xg(x,K_0) - yp(x) < 0$ and so solutions move to the left. Hence for a trajectory starting at (x,y), $x > K_0$, $y > 0$ we have

$$-\sup_{K_0 \le u \le x} \frac{-s + cp(u)}{p(u)} \le \frac{dy}{dx} < 0$$

so long as the trajectory remains to the right of K_0. It follows that all solutions starting to the right of K_0 move to the left with bounded slopes and so must cross the line $x = K_0$ (with negative slope) in finite time.

In order to consider the case $x < K_0$ we plot the predator and prey isoclines (see Fig. 1), i.e. the curves given by putting $y' = x' = 0$. The predator isocline is the line $x = a$ (C_1 in Fig.); trajectories crossing this line do so with a horizontal tangent. The prey isocline is given by $y = sg(x,K_0)/p(x)$. Let C_2 in the figure represent such a curve; trajectories will cross this curve with a vertical tangent. We divide $0 < x < K_0$, $y > 0$ into four regions:

Region I $= \{(x,y): a < x < K_0,\ y > xg(x,K_0)/p(x)\}$

Region II $= \{(x,y): 0 < x < a,\ y > xg(x,K_0)/p(x)\}$

Region III $= \{(x,y): 0 < x < a,\ y < xg(x,K_0)/p(x)\}$

Region IV $= \{(x,y): a < x < K_0,\ y < xg(x,K_0)/p(x)\}$

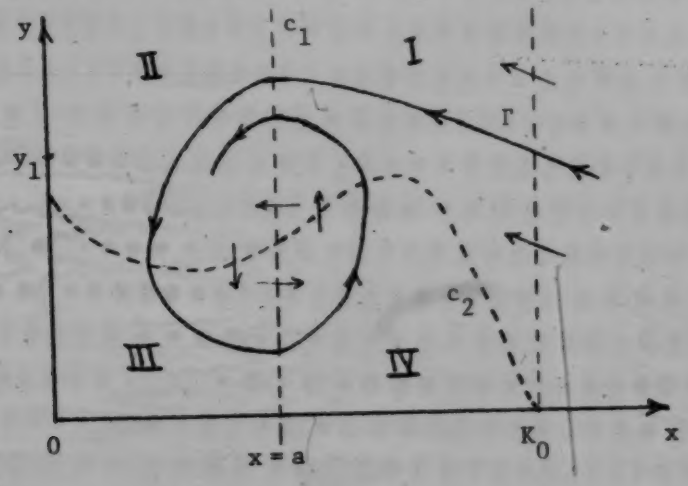

Fig. 1.

From (1.3) it is readily seen that $dy/dx < 0$ in regions I and III, whereas $dy/dx > 0$ in regions II and IV. Also, from (1.1a), $x' < 0$ for $y > xg(x,K_0)/p(x)$ and $x' > 0$ for $0 < y < xg(x,K_0)/p(x)$, $0 < x < K$.

Consider now a trajectory crossing $x = K_0$ at $y = y_1$ into region I, where $y_1 > \max_{0\le x\le K} xg(x,K_0)/p(x)$. Denote this trajectory by Γ. Then Γ continues to the left with negative slope. By (1.3), since

$$\inf_{\substack{a\le x\le K_0 \\ y\ge y_1}} \frac{-s + cp(x)}{xg(x,K_0)/y - p(x)} \le \frac{dy}{dx} < 0$$

for Γ so long as it remains in region I, Γ must cross C_1 in finite time and pass into region II. Here the trajectory Γ continues to the left but with a positive slope. Since it cannot intersect the y-axis, it must cross C_2 in finite time and pass into region III; here the trajectory Γ moves to the right with negative slope. Again, since it cannot intersect either axis, it must cross C_1 in finite time and pass into region IV. Since Γ cannot intersect the x-axis, nor cross the line $x = K_0$, it must cross C_2 again in finite time and pass back into region I.

By the uniqueness of initial-value problems, Γ cannot intersect itself and so must cross C_1 once more below its first crossing. Continuing this process we deduce that the positive limit set of Γ, $L(\Gamma^+)$, lies in a compact region interior to the set $\{(x,y): 0 < x < K_0, y > 0\}$. Hence we arrive at the conclusion that $L(\Gamma^+)$ is a nonempty, closed and connected set (see [1], chap. 16).

1.6. Results of thesis. We have seen that in the autonomous case, i.e. with a constant carrying capacity, there exists an equilibrium inside the first quadrant whose stability properties can be determined by imposing

conditions on the specific growth rate function and the predator response function.

In what follows it is shown that, when the equilibrium is slightly perturbed (by introducing a periodic carrying capacity of small fluctuations) it becomes a periodic solution in almost all cases, and that the stability properties of these periodic solutions are preserved.

Furthermore, if we assume that we have a limit cycle in the autonomous case (as obtained in Chapter I) and then consider the nonautonomous case with the assumption that the carrying capacity has the same period as the limit cycle, we find that there exists a perturbed limit cycle which retains the same stability properties as the unperturbed one.

This means that biologically, in almost all cases, the essential dynamics of the population behaviour is preserved.

CHAPTER II

In this chapter we are interested in looking at periodic solutions which are basically perturbed from the equilibrium (a,b) of the autonomous system. Since we wish to make use of the Implicit Function Theorem to find such solutions, we must consider the variational system. We find that this gives rise to four different cases, depending on the relative values of g, p and K; we investigate the stability properties of these cases, and then consider the application of these results to a specific example.

2.1. The variational equation. Let $x(t,\xi,\eta,\varepsilon)$, $y(t,\xi,\eta,\varepsilon)$ be a solution of (1.1) such that

$$x(0,\xi,\eta,\varepsilon) = a + \xi, \quad y(0,\xi,\eta,\varepsilon) = b + \eta.$$

Let

$$F(\xi,\eta,\varepsilon) = x(\omega,\xi,\eta,\varepsilon) - a - \xi$$

(2.1)

$$G(\xi,\eta,\varepsilon) = y(\omega,\xi,\eta,\varepsilon) - b - \eta.$$

We wish to solve $F(\xi,\eta,\varepsilon) = G(\xi,\eta,\varepsilon) = 0$ in order to obtain ξ, η as functions of ε; when this is done we will have found a periodic solution.

Now $F(0,0,0) = x(\omega,0,0,0) - a = 0$

$G(0,0,0) = y(\omega,0,0,0) - b = 0$

$F_\xi(0,0,0) = x_\xi(\omega,0,0,0) - 1$

$G_\xi(0,0,0) = y_\xi(\omega,0,0,0)$

x_ξ, y_ξ satisfy the variational system

$$x'_\xi = H(x,K)x_\xi - p(x)y_\xi$$

$$y'_\xi = cyp_x(x)x_\xi + \big(-s+cp(x)\big)y_\xi$$

$$x_\xi(0) = 1, \quad y_\xi(0) = 0,$$

where $H(x,K) = g(x,K) + xg_x(x,K) - xg(x,K)p_x(x)/p(x)$.

At $\xi = \eta = \varepsilon = 0$ we have

(2.2a) $$x'_\xi = H(a,K_0)x_\xi - p(a)y_\xi$$

(2.2b) $$y'_\xi = bcp_x(a)x_\xi \ .$$

Differentiating (2.2a) and using (2.2b) we have

$$x''_\xi - H(a,K_0)x'_\xi + bcp(a)p_x(a)x_\xi = 0$$

Since $H(a,K_0)$, $p(a)$, $p_x(a)$ are constants we obtain the solution

(2.3) $$x_\xi = c_1e^{\rho_1 t} + c_2e^{\rho_2 t}$$

where c_1, c_2 are constants and

(2.4) $$\rho_1,\rho_2 = \frac{1}{2}\big(H_0 \pm \sqrt{H_0^2 - 4bcpp_x}\ \big)$$

where $H_0 = H(a,K_0)$, $p = p(a)$, $p_x = p_x(a)$, these now being constants.

The following four cases arise:

2.2. <u>Case I</u>. $H_0^2 > 4bcpp_x$.

Differentiating (2.3)

$$x'_\xi = \rho_1c_1e^{\rho_1 t} + \rho_2c_2e^{\rho_2 t}$$

$$= H_0x_\xi - py_\xi \qquad \text{(using (2.2a))}$$

$$x_\xi(0) = 1 \Rightarrow c_1 + c_2 = 1$$

$$x'_\xi(0) = H_0 \Rightarrow \rho_1c_1 + \rho_2c_2 = H_0 \qquad \Rightarrow c_1 = \frac{\rho_1}{\rho_1-\rho_2}, \quad c_2 = \frac{-\rho_2}{\rho_1-\rho_2}.$$

Hence

$$(2.5) \qquad x_\xi = \frac{\rho_1 e^{\rho_1 t} - \rho_2 e^{\rho_2 t}}{(H_0^2 - 4bcpp_x)^{\frac{1}{2}}}, \quad \text{since} \quad \rho_1 - \rho_2 = (H_0^2 - 4bcpp_x)^{\frac{1}{2}}.$$

From (2.2a)

$$y_\xi = \frac{1}{p}(H_0 x_\xi - x_\xi')$$
$$= \frac{1}{p}\frac{\rho_1\rho_2}{\rho_1 - \rho_2}(e^{\rho_1 t} - e^{\rho_2 t})$$

$$(2.6) \quad \text{i.e.} \quad y_\xi = \frac{bcp_x}{(H_0^2 - 4bcpp_x)^{\frac{1}{2}}}(e^{\rho_1 t} - e^{\rho_2 t})$$

since $\rho_1 + \rho_2 = H_0$ and $\rho_1\rho_2 = bcpp_x$. Now

$$F_\eta(0,0,0) = x_\eta(\omega,0,0,0), \qquad x_\eta(0) = 0$$
$$G_\eta(0,0,0) = y_\eta(\omega,0,0,0) - 1, \quad y_\eta(0) = 1$$

and we obtain in a similar way

$$(2.7) \qquad x_\eta = \frac{p(e^{\rho_2 t} - e^{\rho_1 t})}{(H_0^2 - 4bcpp_x)^{\frac{1}{2}}}$$

$$(2.8) \qquad y_\eta = \frac{\rho_1 e^{\rho_2 t} - \rho_2 e^{\rho_1 t}}{(H_0^2 - 4bcpp_x)^{\frac{1}{2}}}.$$

Hence

$$(2.9a) \qquad F_\xi(0,0,0) = \frac{\rho_1 e^{\rho_1\omega} - \rho_2 e^{\rho_2\omega}}{(H_0^2 - 4bcpp_x)^{\frac{1}{2}}} - 1$$

$$(2.9b) \qquad G_\xi(0,0,0) = \frac{bcp_x(e^{\rho_1\omega} - e^{\rho_2\omega})}{(H_0^2 - 4bcpp_x)^{\frac{1}{2}}}$$

$$(2.9c) \qquad F_\eta(0,0,0) = \frac{p(e^{\rho_2\omega} - e^{\rho_1\omega})}{(H_0^2 - 4bcpp_x)^{\frac{1}{2}}}$$

$$(2.9d)\qquad G_\eta(0,0,0) = \frac{\rho_1 e^{\rho_2\omega} - \rho_2 e^{\rho_1\omega}}{(H_0^2 - 4bcpp_x)^{\frac{1}{2}}} - 1$$

Let

$$J = \begin{pmatrix} F_\xi(0,0,0) & F_\eta(0,0,0) \\ G_\xi(0,0,0) & G_\eta(0,0,0) \end{pmatrix}$$

$$\det J = \left(\frac{\rho_1 e^{\rho_1\omega} - \rho_2 e^{\rho_2\omega}}{\rho_1 - \rho_2} - 1\right)\left(\frac{\rho_1 e^{\rho_2\omega} - \rho_2 e^{\rho_1\omega}}{\rho_1 - \rho_2} - 1\right) + \rho_1\rho_2 \frac{(e^{\rho_1\omega} - e^{\rho_2\omega})^2}{(\rho_1 - \rho_2)^2}$$

$$= e^{(\rho_1+\rho_2)\omega} - e^{\rho_1\omega} - e^{\rho_2\omega} + 1$$

$$(2.10)\quad \text{i.e. } \det J = (e^{\rho_1\omega} - 1)(e^{\rho_2\omega} - 1) \neq 0 \text{ for any } \omega > 0 .$$

Now

$$F_\varepsilon(0,0,0) = x_\varepsilon(\omega,0,0,0)$$

$$G_\varepsilon(0,0,0) = y_\varepsilon(\omega,0,0,0) \qquad \text{(from (2.1))}$$

x_ε, y_ε satisfy the variational equations

$$x_\varepsilon' = H(x,K)x_\varepsilon - p(x)y_\varepsilon + xg_K(x,K)\kappa(t)$$

$$y_\varepsilon' = cyp_x(x)x_\varepsilon + \big(-s + cp(x)\big)y_\varepsilon$$

$$x_\varepsilon(0) = y_\varepsilon(0) = 0.$$

At $\xi = \eta = \varepsilon = 0$ we have

$$x_\varepsilon' = H(a,K_0)x_\varepsilon - p(a)y_\varepsilon + ag_K(a,K_0)\kappa(t)$$

$$y_\varepsilon' = bcp_x(a)x_\varepsilon .$$

The solution is given by (see [1] chap. 3)

$$\begin{pmatrix} x_\varepsilon(t,0,0,0) \\ y_\varepsilon(t,0,0,0) \end{pmatrix} = e^{tB}\int_0^t e^{-rB}\begin{pmatrix} ag_K(a,K_0)\kappa(r) \\ 0 \end{pmatrix} dr$$

where

$$B = \begin{pmatrix} H(a,K_0) & -p(a) \\ bcp_x(a) & 0 \end{pmatrix}$$

Now e^{tB} is the fundamental matrix for the linear system (2.2) (see [1] chap. 3) i.e.

$$e^{tB} = \begin{pmatrix} x_\xi & x_\eta \\ y_\xi & y_\eta \end{pmatrix},$$

where x_ξ, x_η, y_ξ, y_η are given by (2.5), (2.7), (2.6), (2.8). Hence

$$\begin{pmatrix} x_\varepsilon(t,0,0,0) \\ y_\varepsilon(t,0,0,0) \end{pmatrix} = \begin{pmatrix} x_\xi & x_\eta \\ y_\xi & y_\eta \end{pmatrix} \int_0^t \Delta^{-1} \begin{pmatrix} y_\eta & -x_\eta \\ -y_\xi & x_\xi \end{pmatrix} \begin{pmatrix} ag_K\,\kappa(r) \\ 0 \end{pmatrix} dr$$

where

$$\Delta = \begin{vmatrix} x_\xi & x_\eta \\ y_\xi & y_\eta \end{vmatrix} = \frac{1}{(\rho_1-\rho_2)^2} [(\rho_1^2+\rho_2^2)e^{(\rho_1+\rho_2)r} - \rho_1\rho_2(e^{2\rho_1 r} + e^{2\rho_2 r}) + \rho_1\rho_2(e^{\rho_1 r} - e^{\rho_2 r})^2]$$

$$= e^{(\rho_1+\rho_2)r}$$

i.e. $\Delta = e^{H_0 r}$.

Hence we obtain

$$(2.11) \quad \begin{pmatrix} F_\varepsilon(0,0,0) \\ G_\varepsilon(0,0,0) \end{pmatrix} = ag_K(a,K_0) \begin{pmatrix} x_\xi(\omega,0,0,0) & x_\eta(\omega,0,0,0) \\ y_\xi(\omega,0,0,0) & y_\eta(\omega,0,0,0) \end{pmatrix} \int_0^\omega e^{-H_0 t} \kappa(t) \begin{pmatrix} y_\eta(t) \\ -y_\xi(t) \end{pmatrix} dt.$$

2.3. Case II. $H_0^2 = 4bcpp_x$, $H_0 \neq 0$.

The solution of (2.2) is given by

$$x_\xi = c_1 e^{\frac{1}{2}H_0 t} + c_2 t\, e^{\frac{1}{2}H_0 t}, \quad c_1 \text{ and } c_2 \text{ constants}$$

and so

$$x_\xi' = \tfrac{1}{2}H_0 c_1 e^{\frac{1}{2}H_0 t} + \tfrac{1}{2}H_0 c_2 t\, e^{\frac{1}{2}H_0 t} + c_2 e^{\frac{1}{2}H_0 t}$$

$$x_\xi(0) = 1 \quad \text{and} \quad x_\xi'(0) = H_0 \Rightarrow c_1 = 1 \quad \text{and} \quad c_2 = \tfrac{1}{2}H_0.$$

Hence

$$(2.12) \qquad x_\xi = (1 + \tfrac{1}{2}H_0 t)e^{\frac{1}{2}H_0 t}.$$

From (2.2a), $py_\xi = H_0 x_\xi - x_\xi'$, giving

$$(2.13) \qquad y_\xi = \frac{H_0^2}{4p}\, t\, e^{\frac{1}{2}H_0 t}$$

In a similar manner we obtain

$$(2.14) \qquad x_\eta = -pt\, e^{\frac{1}{2}H_0 t}$$

$$(2.15) \qquad y_\eta = (1 - \tfrac{1}{2}H_0 t)e^{\frac{1}{2}H_0 t}$$

Hence

$$(2.16a) \qquad F_\xi(0,0,0) = (1 + \tfrac{1}{2}H_0\omega)e^{\frac{1}{2}H\omega} - 1$$

$$(2.16b) \qquad G_\xi(0,0,0) = \frac{H_0^2}{4p}\, \omega\, e^{\frac{1}{2}H_0\omega}$$

$$(2.16c) \qquad F_\eta(0,0,0) = -p\omega\, e^{\frac{1}{2}H_0\omega}$$

$$(2.16d) \qquad G_\eta(0,0,0) = (1 - \tfrac{1}{2}H_0\omega)e^{\frac{1}{2}H_0\omega} - 1,$$

and

$$(2.17) \qquad \det J = (1 - \tfrac{1}{4}H_0^2\omega^2)e^{H_0\omega} - 2e^{\frac{1}{2}H_0\omega} + 1 + \tfrac{1}{4}H_0^2\omega^2 e^{H_0\omega}$$

$$= (e^{\frac{1}{2}H_0\omega} - 1)^2 \neq 0 \quad \text{for any} \quad \omega > 0 \quad (H_0 \neq 0)$$

The values for $F_\varepsilon(0,0,0)$ and $G_\varepsilon(0,0,0)$ turn out to be exactly the same as for case I and are given by (2.11), but using the values of x_ξ, x_η,

y_ξ, y_η given by (2.12)-(2.15).

2.4. Case III. $H_0^2 < 4bcpp_x$, $H_0 \neq 0$.

Let $H_0^2 - 4bcpp_x = -\mu^2$ so that, from (2.4),

$$\rho_1 = \tfrac{1}{2}(H_0 + i\mu), \quad \rho_2 = \tfrac{1}{2}(H_0 - i\mu).$$

Hence

$$x_\xi = e^{\frac{1}{2}H_0 t}\left(c_1 \cos\frac{\mu t}{2} + c_2 \sin\frac{\mu t}{2}\right), \quad c_1 \text{ and } c_2 \text{ constants}$$

$$x_\xi' = \tfrac{1}{2}H_0 e^{\frac{1}{2}H_0 t}\left(c_1 \cos\frac{\mu t}{2} + c_2 \sin\frac{\mu t}{2}\right) + e^{\frac{1}{2}H_0 t}\left(\frac{\mu c_2}{2}\cos\frac{\mu t}{2} - \frac{\mu c_1}{2}\sin\frac{\mu t}{2}\right)$$

and

$$x_\xi(0) = 1, \quad x_\xi'(0) = H_0 \Rightarrow c_1 = 1, \quad c_2 = \frac{H_0}{\mu}$$

so that

$$(2.18) \qquad x_\xi = e^{\frac{1}{2}H_0 t}\left(\cos\frac{\mu t}{2} + \frac{H_0}{\mu}\sin\frac{\mu t}{2}\right)$$

and

$$(2.19) \qquad y_\xi = \frac{2bcp_x}{\mu} e^{\frac{1}{2}H_0 t} \sin\frac{\mu t}{2} \qquad \text{(from (2.2a))}.$$

Similarly

$$(2.20) \qquad x_\eta = -\frac{2p}{\mu} e^{\frac{1}{2}H_0 t} \sin\frac{\mu t}{2}$$

$$(2.21) \qquad y_\eta = e^{\frac{1}{2}H_0 t}\left(\cos\frac{\mu t}{2} - \frac{H_0}{\mu}\sin\frac{\mu t}{2}\right)$$

Hence

$$(2.22a) \qquad F_\xi(0,0,0) = e^{\frac{1}{2}H_0\omega}\left(\cos\frac{\mu\omega}{2} + \frac{H_0}{\mu}\sin\frac{\mu\omega}{2}\right) - 1$$

$$(2.22b) \qquad G_\xi(0,0,0) = \frac{2bcp_x}{\mu} e^{\frac{1}{2}H_0\omega} \sin\frac{\mu\omega}{2}$$

$$(2.22c)\qquad F_\eta(0,0,0) = -\frac{2p}{\mu}\, e^{\frac{1}{2}H_0\omega} \sin\frac{\mu\omega}{2}$$

$$(2.22d)\qquad G_\eta(0,0,0) = e^{\frac{1}{2}H_0\omega}\left(\cos\frac{\mu\omega}{2} - \frac{H_0}{\mu}\sin\frac{\mu\omega}{2}\right) - 1$$

$$\det J = e^{H_0\omega}\left(\cos^2\frac{\mu\omega}{2} - \frac{H_0^2}{\mu^2}\sin^2\frac{\mu\omega}{2}\right) - 2e^{\frac{1}{2}H_0\omega}\cos\frac{\mu\omega}{2} + 1$$

$$+ \frac{4bcpp_x}{\mu^2}\, e^{H_0\omega}\sin^2\frac{\mu\omega}{2}$$

$$= e^{H_0\omega} - 2e^{\frac{1}{2}H_0\omega}\cos\frac{\mu\omega}{2} + 1.$$

Thus

$$\det J \geq e^{H_0\omega} - 2e^{\frac{1}{2}H_0\omega} + 1$$

$$= (e^{\frac{1}{2}H_0\omega} - 1)^2 > 0 \quad \text{for any } \omega > 0 \quad (H_0 \neq 0).$$

To compute $F_\varepsilon(0,0,0)$ and $G_\varepsilon(0,0,0)$ we go through the same procedure as in case I and their values are again given by (2.11), but using the values of x_ξ, x_η, y_ξ, y_η given by (2.18)-(2.21).

2.5. Case IV. $H_0 = 0$ so that $\rho_1, \rho_2 = \pm i\sqrt{bcpp_x}$ (from (2.4)).

Let $bcpp_x = \nu^2$. Then

$$x_\xi = c_1 \cos \nu t + c_2 \sin \nu t$$

$$x_\xi' = -\nu c_1 \sin \nu t + \nu c_2 \cos \nu t$$

$$x_\xi(0) = 1, \quad x_\xi'(0) = H_0 \Rightarrow c_1 = 1, \quad c_2 = 0.$$

Thus

$$(2.23)\qquad x_\xi = \cos \nu t \quad \text{and}$$

$$(2.24)\qquad y_\xi = \frac{\nu}{p}\sin \nu t \quad \text{(from (2.2a))}$$

Similarly

$$(2.25) \qquad x_\eta = -\frac{p}{\nu}\sin \nu t$$

$$(2.26) \qquad y_\eta = \cos \nu t \ .$$

Hence

$$(2.27a) \qquad F_\xi(0,0,0) = \cos \nu\omega - 1$$

$$(2.27b) \qquad G_\xi(0,0,0) = \frac{\nu}{p}\sin \nu\omega$$

$$(2.27c) \qquad F_\eta(0,0,0) = -\frac{p}{\nu}\sin \nu\omega$$

$$(2.27d) \qquad G_\eta(0,0,0) = \cos \nu\omega - 1$$

$$\det J = (\cos \nu\omega - 1)^2 + \sin^2 \nu\omega$$

$$(2.28) \qquad \det J = 2(1 - \cos \nu\omega).$$

For any $\omega > 0$, $\det J = 0$ if $\nu = \frac{2n\pi}{\omega}$ (n an integer), i.e. $\det J = 0$ if $bcpp_x = 4n^2\pi^2/\omega^2$, thus giving rise to a critical case when the Implicit Function Theorem is made use of in attempting to express ξ and η as functions of ε.

To derive $F_\varepsilon(0,0,0)$ and $G_\varepsilon(0,0,0)$ in this case, we observe that

$$\Delta = \begin{vmatrix} x_\xi & x_\eta \\ y_\xi & y_\eta \end{vmatrix} = \begin{vmatrix} \cos \nu r & -\frac{p}{\nu}\sin \nu r \\ \frac{\nu}{p}\sin \nu r & \cos \nu r \end{vmatrix} = 1$$

Hence

$$(2.29) \qquad \begin{pmatrix} F_\varepsilon(0,0,0) \\ G_\varepsilon(0,0,0) \end{pmatrix} = ag_K(a,K_0) \begin{pmatrix} x_\xi(\omega,0,0,0) & x_\eta(\omega,0,0,0) \\ y_\xi(\omega,0,0,0) & y_\eta(\omega,0,0,0) \end{pmatrix} \int_0^\omega \kappa(t) \begin{pmatrix} y_\eta(t) \\ -y_\xi(t) \end{pmatrix} dt$$

$$= ag_K(a,K_0) \begin{pmatrix} x_\xi & x_\eta \\ y_\xi & y_\eta \end{pmatrix} \int_0^\omega \kappa(t) \begin{pmatrix} \cos \nu t \\ -\frac{\nu}{p}\sin \nu t \end{pmatrix} dt \ .$$

Thus if $\nu = 2n\pi/\omega$ (n an integer) we may have two possibilities:

(i) $F_\varepsilon(0,0,0) = G_\varepsilon(0,0,0) = 0$

(ii) at least one of $F_\varepsilon(0,0,0)$, $G_\varepsilon(0,0,0)$ is nonzero.

To see how these possibilities arise one would have to consider a specific example, where the values of g, p and κ are given explicitly.

If case (i) occurs, then we need to consider the critical case of the Implicit Function Theorem which begins with quadratic terms: whereas if case (ii) holds, then we require the third critical case of the Implicit Function Theorem (see Freedman [4]). In either case, we would need to compute second partial derivatives of F, G.

2.6. Existence of periodic solutions. In order to obtain $\xi(\varepsilon)$, $\eta(\varepsilon)$ by the Implicit Function Theorem we write

$$\begin{pmatrix}\xi(\varepsilon)\\ \eta(\varepsilon)\end{pmatrix} = \begin{pmatrix}\xi(0)\\ \eta(0)\end{pmatrix} + \frac{d}{d\varepsilon}\begin{pmatrix}\xi(0)\\ \eta(0)\end{pmatrix}\varepsilon + \frac{1}{2}\frac{d^2}{d\varepsilon^2}\begin{pmatrix}\xi(0)\\ \eta(0)\end{pmatrix}\varepsilon^2 + \cdots$$

(by Taylor's Theorem).

Now $\begin{pmatrix}\xi(0)\\ \eta(0)\end{pmatrix} = \begin{pmatrix}0\\ 0\end{pmatrix}$, and $F(\xi,\eta,\varepsilon) = G(\xi,\eta,\varepsilon) = 0$

$$\Rightarrow \quad F_\xi\xi_\varepsilon + F_\eta\eta_\varepsilon = -F_\varepsilon$$

$$G_\xi\xi_\varepsilon + G_\eta\eta_\varepsilon = -G_\varepsilon$$

i.e. $$\begin{pmatrix}F_\xi & F_\eta\\ G_\xi & G_\eta\end{pmatrix}\begin{pmatrix}\xi_\varepsilon\\ \eta_\varepsilon\end{pmatrix} = -\begin{pmatrix}F_\varepsilon\\ G_\varepsilon\end{pmatrix}$$ or

$$\begin{pmatrix}\xi_\varepsilon(0)\\ \eta_\varepsilon(0)\end{pmatrix} = -J^{-1}\begin{pmatrix}F_\varepsilon\\ G_\varepsilon\end{pmatrix}, \quad \det J \neq 0 \text{ for cases I, II, III.} \tag{2.30}$$

Hence, for cases I, II, III,

$$(2.31)\qquad \begin{pmatrix}\xi(\varepsilon)\\ \eta(\varepsilon)\end{pmatrix} = -J^{-1}\begin{pmatrix}F_\varepsilon(0,0,0)\\ G_\varepsilon(0,0,0)\end{pmatrix}\varepsilon + o(\varepsilon).$$

Since $J = \begin{pmatrix}x_\xi - 1 & x_\eta\\ y_\xi & y_\eta - 1\end{pmatrix}$ we obtain, using (2.11)

$$\begin{pmatrix}\xi(\varepsilon)\\ \eta(\varepsilon)\end{pmatrix} = \frac{-\varepsilon a g_K(a,K_0)}{\det J}\left[(x_\xi y_\eta - x_\eta y_\xi)\begin{pmatrix}1 & 0\\ 0 & 1\end{pmatrix} - \begin{pmatrix}x_\xi & x_\eta\\ y_\xi & y_\eta\end{pmatrix}\right]\int_0^\omega e^{-H_0\omega_K(s)}\begin{pmatrix}y_\eta(s)\\ -y_\xi(s)\end{pmatrix}ds + o(\varepsilon)$$

from which we can compute $\xi(\varepsilon)$, $\eta(\varepsilon)$ after inserting the appropriate values of x_ξ, x_η, y_ξ, y_η for each of the cases I, II, III. For case IV we need second derivatives of F, G.

2.7. Stability of the periodic solutions. For system (1.1) consider a periodic solution

$$\phi(t,\varepsilon) = x(t,\xi,\eta,\varepsilon)$$

$$\psi(t,\varepsilon) = y(t,\xi,\eta,\varepsilon), \text{ of period } \omega, \text{ and let}$$

$$\phi(t,\varepsilon) = \phi_0(t) + \varepsilon\phi_1(t) + o(\varepsilon), \quad \phi_0(t) \equiv a$$

$$\psi(t,\varepsilon) = \psi_0(t) + \varepsilon\psi_1(t) + o(\varepsilon), \quad \psi_0(t) \equiv b.$$

The variational equations for system (1.1) with respect to ϕ, ψ are

$$(2.32a)\qquad u' = H(\phi,K)u - p(\phi)v$$

$$(2.32b)\qquad v' = c\psi p_x(\phi)u + \big(-s + cp(\phi)\big)v$$

where $H(\phi,K) = g(\phi,K) + \phi g_x(\phi,K) - \phi g(\phi,K)p_x(\phi)/p(\phi)$. Let

$$(2.33)\qquad u = u_0 + u_1\varepsilon + o(\varepsilon), \quad v = v_0 + v_1\varepsilon + o(\varepsilon)$$

$$H(\phi,K) = H(a,K_0) + \varepsilon \frac{d}{d\varepsilon} H(\phi,K)\Big|_{\varepsilon=0} + o(\varepsilon)$$

$$p(\phi) = p(a) + \varepsilon \frac{d}{d\varepsilon} p(\phi)\Big|_{\varepsilon=0} + o(\varepsilon) .$$

Let

$$(2.34) \qquad \Phi(t,\varepsilon) = \Phi_0(t) + \varepsilon\Phi_1(t) + o(\varepsilon)$$

be a fundamental matrix for (2.32), $\Phi(0,\varepsilon) = I$, the identity matrix, and take the initial conditions $\begin{pmatrix} u_0(0) \\ v_0(0) \end{pmatrix}$ to be $\begin{pmatrix} 1 \\ 0 \end{pmatrix}$ and $\begin{pmatrix} 0 \\ 1 \end{pmatrix}$; $\begin{pmatrix} u_1(0) \\ v_1(0) \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$ for $i = 1,2,\cdots$. Substituting in (2.32) we have

$$u_0' + u_1'\varepsilon + o(\varepsilon) = [H(a,K_0) + \varepsilon \frac{d}{d\varepsilon} H(\phi,K)\Big|_{\varepsilon=0} + o(\varepsilon)]\big(u_0 + u_1\varepsilon + o(\varepsilon)\big)$$

$$- [p(a) + \varepsilon \frac{d}{d\varepsilon} p(\phi)\Big|_{\varepsilon=0} + o(\varepsilon)]\big(v_0 + v_1\varepsilon + o(\varepsilon)\big)$$

$$v_0' + v_1'\varepsilon + o(\varepsilon) = [bcp_x(a) + \varepsilon \frac{d}{d\varepsilon} c\psi p_x(\phi)\Big|_{\varepsilon=0} + o(\varepsilon)]\big(u_0 + u_1\varepsilon + o(\varepsilon)\big)$$

$$+ [-s + cp(a) + \varepsilon \frac{d}{d\varepsilon}\big(-s + cp(\phi)\big)\Big|_{\varepsilon=0} + o(\varepsilon)]\big(v_0 + v_1\varepsilon + o(\varepsilon)\big).$$

Comparing coefficients we have

$$u_0' = H(a,K_0)u_0 - p(a)v_0$$

$$v_0' = bcp_x(a)u_0 .$$

Hence $\Phi_0(t) = \begin{pmatrix} x_\xi & x_\eta \\ y_\xi & y_\eta \end{pmatrix}$, $\Phi_0(\omega) = e^{\omega B}$

where $B = \begin{pmatrix} H(a,K_0) & -p(a) \\ bcp_x(a) & 0 \end{pmatrix}$. (Cf. §2.1-2.5).

We also have

$$u_1' = H(a,K_0)u_1 - p(a)v_1 + \frac{d}{d\varepsilon} H(\phi,K)\Big|_{\varepsilon=0} u_0 - \frac{d}{d\varepsilon} p(\phi)\Big|_{\varepsilon=0} v_0$$

$$v_1' = bcp_x(a)u_1 + \frac{d}{d\varepsilon} c\psi p_x(\phi)\Big|_{\varepsilon=0} u_0 + \frac{d}{d\varepsilon}\big(-s + cp(\phi)\big)\Big|_{\varepsilon=0} v_0.$$

But $\frac{d}{d\varepsilon} H(\phi,K) = H_x(\phi,K)\phi_\varepsilon + H_K(\phi,K)\kappa(t)$

and $\frac{d}{d\varepsilon} H(\phi,K)\Big|_{\varepsilon=0} = H_x(a,K_0)\phi_1(t) + H_K(a,K_0)\kappa(t)$

$$\therefore\ u_1' = H(a,K_0)u_1 - p(a)v_1 + [H_x(a,K_0)\phi_1(t) + H_K(a,K_0)\kappa(t)]u_0 - p_x(a)\phi_1(t)v_0$$

$$v_1' = bcp_x(a)u_1 + [c\psi p_{xx}(a)\phi_1(t) + cp_x(a)\psi_1(t)]u_0 + cp_x(a)\phi_1(t)v_0.$$

Since i.c.'s are $\begin{pmatrix} u_1(0) \\ v_1(0) \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$ and $\begin{pmatrix} u_1 \\ v_1 \end{pmatrix}' = B\begin{pmatrix} u_1 \\ v_1 \end{pmatrix} + f(t)$, where

$$B = \begin{pmatrix} H(a,K_0) & -p(a) \\ bcp_x(a) & 0 \end{pmatrix} \quad \text{and}$$

$$f(t) = \begin{pmatrix} H_x(a,K_0)\phi_1(t) + H_K(a,K_0)\kappa(t) & -p_x(a)\phi_1(t) \\ c\psi p_{xx}(a)\phi_1(t) + cp_x(a)\psi_1(t) & cp_x(a)\phi_1(t) \end{pmatrix} \begin{pmatrix} u_0 \\ v_0 \end{pmatrix}$$

the solution is given by

$$(2.35) \qquad \begin{pmatrix} u_1(t) \\ v_1(t) \end{pmatrix} = e^{tB} \int_0^t e^{-rB} f(r)dr \qquad \text{(see [1] chap. 3)} \quad \text{and}$$

$$e^{tB} = \begin{pmatrix} x_\xi & x_\eta \\ y_\xi & y_\eta \end{pmatrix}.$$

Since $\det e^{tB} = e^{tH_0}$ we have

$$\begin{pmatrix} u_1 \\ v_1 \end{pmatrix} = \begin{pmatrix} x_\xi & x_\eta \\ y_\xi & y_\eta \end{pmatrix} \int_0^t e^{-rH_0} \begin{pmatrix} y_\eta & -x_\eta \\ -y_\xi & x_\xi \end{pmatrix} f(r)dr\ .$$

In order to find the eigenvalues of $\phi(\omega,\varepsilon)$ we suppose that

$$\Phi_1(\omega) = \begin{pmatrix} \alpha & \beta \\ \gamma & \delta \end{pmatrix} .$$

Then, using (2.34), we derive for the eigenvalues λ

$$\det \begin{pmatrix} x_\xi + \alpha\varepsilon + o(\varepsilon) - \lambda & x_\eta + \beta\varepsilon + o(\varepsilon) \\ y_\xi + \gamma\varepsilon + o(\varepsilon) & y_\eta + \delta\varepsilon + o(\varepsilon) - \lambda \end{pmatrix} = 0$$

or

$$\lambda^2 - \big(x_\xi + y_\eta + (\alpha+\delta)\varepsilon + o(\varepsilon)\big)\lambda + x_\xi y_\eta - x_\eta y_\xi + (y_\eta\alpha + x_\xi\delta - x_\eta\gamma - y_\xi\beta)\varepsilon + o(\varepsilon) = 0$$

$$\therefore \quad \lambda = \tfrac{1}{2}\big(x_\xi + y_\eta + (\alpha+\delta)\varepsilon + o(\varepsilon)\big)$$

$$\pm \tfrac{1}{2}\left\{(x_\xi+y_\eta)^2 - 4(x_\xi y_\eta - x_\eta y_\xi) + 2\varepsilon[(x_\xi - y_\eta)(\alpha-\delta) + 2(x_\eta\gamma + y_\xi\beta)] + o(\varepsilon)\right\}^{\frac{1}{2}}.$$

In case $\varepsilon = 0$

$$\lambda = \tfrac{1}{2}(x_\xi+y_\eta) \pm \tfrac{1}{2}\left\{(x_\xi+y_\eta)^2 - 4(x_\xi y_\eta - x_\eta y_\xi)\right\}^{\frac{1}{2}}.$$

<u>Case I</u>. $x_\xi + y_\eta = e^{\rho_1 t} + e^{\rho_2 t}$ (from (2.5),(2.8), since $\rho_1 - \rho_2 = (H_0^2 - 4bcpp_x)^{\frac{1}{2}}$)

$$\therefore \quad \lambda = \tfrac{1}{2}(e^{\rho_1 t} + e^{\rho_2 t}) \pm \tfrac{1}{2}\left\{(e^{\rho_1 t} + e^{\rho_2 t})^2 - 4\Delta\right\}^{\frac{1}{2}}, \quad \Delta = e^{tH_0} .$$

$\lambda = e^{\rho_1 t}$ or $e^{\rho_2 t}$, because $H_0 = \rho_1 + \rho_2$.

Since $\rho_1, \rho_2 = \tfrac{1}{2}\big(H_0 \pm \sqrt{H_0^2 - 4bcpp_x}\big)$, $b,c,p,p_x > 0$, it follows that the real parts of ρ_1, ρ_2 have the same sign as H_0, hence we arrive at the following stability conditions:

(2.36) $\quad H_0 \gtrless 0 \Rightarrow |\lambda| \gtrless 1 \Rightarrow$ instability / asymptotic stability.

Case II. $x_\xi + y_\eta = 2e^{\frac{1}{2}H_0 t}$ (from (2.12), (2.15))

$$\therefore \lambda = e^{\frac{1}{2}H_0 t} \pm \frac{1}{2}\left\{4e^{H_0 t} - 4\Delta\right\}^{\frac{1}{2}}$$

$$\lambda = e^{\frac{1}{2}H_0 t}$$

and stability conditions (2.36) apply.

Case III. $x_\xi + y_\eta = 2e^{\frac{1}{2}H_0 t}\cos\frac{\mu t}{2}$ (from (2.18), (2.21))

Hence

$$\lambda = e^{\frac{1}{2}H_0 t}\left(\cos\frac{\mu t}{2} \pm i \sin\frac{\mu t}{2}\right)$$

and conditions (2.36) again apply.

Hence for cases I, II, III, $|\lambda|$ is either greater than 1 or less than 1. For ε sufficiently small, $|\lambda|$ cannot change from being greater than to being less than 1 (or vice versa), so that the stability property of the solution is unaltered by a small perturbation. By a theorem on stability (see [1] chap. 13) we thus have

$$H_0 \lesseqgtr 0 \Rightarrow \begin{matrix}\text{asymptotic stability} \\ \text{instability.}\end{matrix}$$

Case IV. We shall find here that $|\lambda| = 1$ and so ε (however small) can effect a change in the stability properties of a solution. For (2.34) we have now $\Phi_0(\omega) = \begin{pmatrix}\cos\nu\omega & -\frac{p}{\nu}\sin\nu\omega \\ \frac{\nu}{p}\sin\nu\omega & \cos\nu\omega\end{pmatrix}$, $\nu^2 = bcpp_x$.

Note that $\det \Phi_0(\omega) = 1$.

To find the eigenvalues λ of $\Phi(\omega,\varepsilon)$ we again suppose $\Phi_1(\omega) = \begin{pmatrix}\alpha & \beta \\ \gamma & \delta\end{pmatrix}$. Then

$$\det\begin{pmatrix}\cos\nu\omega + \alpha\varepsilon + o(\varepsilon) - \lambda & -\frac{p}{\nu}\sin\nu\omega + \beta\varepsilon + o(\varepsilon) \\ \frac{\nu}{p}\sin\nu\omega + \gamma\varepsilon + o(\varepsilon) & \cos\nu\omega + \delta\varepsilon + o(\varepsilon) - \lambda\end{pmatrix} = 0$$

$$\lambda^2 - \left(2\cos\nu\omega + (\alpha+\delta)\varepsilon + o(\varepsilon)\right)\lambda + 1 + \varepsilon\left[(\alpha+\delta)\cos\nu\omega + \left(\frac{\gamma p}{\nu} - \frac{\beta\nu}{p}\right)\sin\nu\omega\right] + o(\varepsilon) = 0 .$$

In case $\varepsilon = 0$

$$\lambda^2 - 2\lambda\cos\nu\omega + 1 = 0$$

and

$$\lambda = \cos\nu\omega \pm \sqrt{\cos^2\nu\omega - 1}$$

(i) If $\nu\omega \neq n\pi$ (n an integer) i.e. $\cos^2\nu\omega < 1$,

$$|\lambda| = (\cos^2\nu\omega + 1 - \cos^2\nu\omega)^{\frac{1}{2}} = 1.$$

(ii) If $\nu\omega = n\pi$, i.e. $\cos^2\nu\omega = 1$, $|\lambda| = 1$.

For $\varepsilon \neq 0$

$$\lambda = \cos\nu\omega + \frac{1}{2}(\alpha+\delta)\varepsilon + o(\varepsilon) \pm \left[\cos^2\nu\omega - 1 - \varepsilon\left(\frac{\gamma p}{\nu} - \frac{\beta\nu}{p}\right)\sin\nu\omega + o(\varepsilon)\right]^{\frac{1}{2}}$$

(i) $\nu\omega \neq n\pi$: for small ε, the expression inside radical sign remains negative, and so

$$|\lambda| = \left[\cos^2\nu\omega + (\alpha+\delta)\varepsilon\cos\nu\omega - \cos^2\nu\omega + 1 + \varepsilon\left(\frac{\gamma p}{\nu} - \frac{\beta\nu}{p}\right)\sin\nu\omega + o(\varepsilon)\right]^{\frac{1}{2}}$$

$$|\lambda| = \left(1 + \varepsilon\ell + o(\varepsilon)\right)^{\frac{1}{2}}, \quad \text{where} \quad \ell = (\alpha+\delta)\cos\nu\omega + \left(\frac{\gamma p}{\nu} - \frac{\beta\nu}{p}\right)\sin\nu\omega .$$

Hence $\varepsilon\ell > 0 \Rightarrow |\lambda| > 1 \Rightarrow$ instability

$\varepsilon\ell < 0 \Rightarrow |\lambda| < 1 \Rightarrow$ asymptotic stability.

(ii) $\nu\omega = n\pi$

(a) n even (so $\cos\nu\omega = 1$):

$$\lambda = 1 + \frac{1}{2}(\alpha+\delta)\varepsilon + o(\varepsilon) \pm \left(o(\varepsilon)\right)^{\frac{1}{2}}.$$

(b) n odd (so $\cos\nu\omega = -1$):

$$\lambda = -1 + \frac{1}{2}(\alpha+\delta)\varepsilon + o(\varepsilon) \pm \left(o(\varepsilon)\right)^{\frac{1}{2}} .$$

In order to estimate the contribution that $\left(o(\varepsilon)\right)^{\frac{1}{2}}$ makes to the value of λ we need to consider higher powers of ε in the expansion

for $\Phi(\omega,\varepsilon)$.

Let $\Phi(\omega,\varepsilon) = \Phi_0(\omega) + \varepsilon\Phi_1(\omega) + \varepsilon^2\Phi_2(\omega) + o(\varepsilon^2)$, where

$$\Phi_0(\omega) = \begin{pmatrix} \cos\nu\omega & -\frac{p}{\nu}\sin\nu\omega \\ \frac{\nu}{p}\sin\nu\omega & \cos\nu\omega \end{pmatrix}.$$

Let

$$\Phi_1(\omega) = \begin{pmatrix} \alpha_i & \beta_i \\ \gamma_i & \delta_i \end{pmatrix}, \quad i = 1,2.$$

$$\det \begin{pmatrix} \cos\nu\omega + \alpha_1\varepsilon + \alpha_2\varepsilon^2 + o(\varepsilon^2) - \lambda & -\frac{p}{\nu}\sin\nu\omega + \beta_1\varepsilon + \beta_2\varepsilon^2 + o(\varepsilon^2) \\ \frac{\nu}{p}\sin\nu\omega + \gamma_1\varepsilon + \gamma_2\varepsilon^2 + o(\varepsilon^2) & \cos\nu\omega + \delta_1\varepsilon + \delta_2\varepsilon^2 + o(\varepsilon^2) - \lambda \end{pmatrix} = 0$$

$$\lambda^2 - \left(2\cos\nu\omega + (\alpha_1+\delta_1)\varepsilon + (\alpha_2+\delta_2)\varepsilon^2 + o(\varepsilon^2)\right)\lambda + 1 + \varepsilon\left[(\alpha_1+\delta_1)\cos\nu\omega + \left(\frac{\gamma_1 p}{\nu} - \frac{\beta_1\nu}{p}\right)\sin\nu\omega\right]$$

$$+ \varepsilon^2\left[\alpha_1\delta_1 - \beta_1\gamma_1 + (\alpha_2+\delta_2)\cos\nu\omega + \left(\frac{\gamma_2 p}{\nu} - \frac{\beta_2\nu}{p}\right)\sin\nu\omega\right] + o(\varepsilon^2) = 0$$

$$\lambda = \cos\nu\omega + \tfrac{1}{2}(\alpha_1+\delta_1)\varepsilon + \tfrac{1}{2}(\alpha_2+\delta_2)\varepsilon^2 + o(\varepsilon^2)$$

$$\pm\left[\cos^2\nu\omega - 1 + \left(\frac{\beta_1\nu}{p} - \frac{\gamma_1 p}{\nu}\right)\varepsilon\sin\nu\omega + \varepsilon^2\left\{\frac{(\alpha_1+\delta_1)^2}{4} + \beta_1\gamma_1 - \alpha_1\delta_1 + \left(\frac{\beta_2\nu}{p} - \frac{\gamma_2 p}{\nu}\right)\sin\nu\omega\right\}\right.$$

$$\left. + o(\varepsilon^2)\right]^{\frac{1}{2}}$$

In case $\varepsilon = 0$, $\lambda = \cos\nu\omega \pm \sqrt{\cos^2\nu\omega - 1}$ and $|\lambda| = 1$, as above.

For $\varepsilon \neq 0$:

(i) $\nu\omega \neq n\pi$ (n an integer), already done above.

(ii) $\nu\omega = n\pi$ (n an integer)

(a) n even (so $\cos\nu\omega = 1$)

$$\lambda = 1 + \tfrac{1}{2}(\alpha_1+\delta_1)\varepsilon + \tfrac{1}{2}(\alpha_2+\delta_2)\varepsilon^2 + o(\varepsilon^2) \pm \left[\varepsilon^2\left\{\frac{(\alpha_1+\delta_1)^2}{4} + \beta_1\gamma_1 - \alpha_1\delta_1\right\} + o(\varepsilon^2)\right]^{\frac{1}{2}}$$

i.e. $\lambda = 1 + \frac{1}{2}(\mathrm{tr}\Phi_1)\varepsilon + \frac{1}{2}(\mathrm{tr}\Phi_2)\varepsilon^2 + o(\varepsilon^2) \pm \left[\varepsilon^2\left\{(\tfrac{1}{2}\mathrm{tr}\Phi_1)^2 - \det\Phi_1\right\} + o(\varepsilon^2)\right]^{\frac{1}{2}}$.

Suppose $\det \Phi_1 > 0$: then term under radical $< |\frac{1}{2}(\mathrm{tr}\Phi_1)\varepsilon|$, and so

$$\varepsilon\, \mathrm{tr}\Phi_1 > 0 \Rightarrow |\lambda| > 1 \Rightarrow \text{instability}$$

$$\varepsilon\, \mathrm{tr}\Phi_1 < 0 \Rightarrow |\lambda| < 1 \Rightarrow \text{asymptotic stability.}$$

(b) n odd (so $\cos \nu\omega = -1$)

$$\lambda = -1 + \frac{1}{2}(\mathrm{tr}\Phi_1)\varepsilon + \frac{1}{2}(\mathrm{tr}\Phi_2)\varepsilon^2 + o(\varepsilon^2) \pm [\varepsilon^2\{(\tfrac{1}{2}\mathrm{tr}\Phi_1)^2 - \det \Phi_1\} + o(\varepsilon^2)]^{\frac{1}{2}}.$$

With $\det \Phi_1 > 0$ we have

$$\varepsilon\, \mathrm{tr}\Phi_1 > 0 \Rightarrow |\lambda| < 1 \Rightarrow \text{asymptotic stability}$$

$$\varepsilon\, \mathrm{tr}\Phi_1 < 0 \Rightarrow |\lambda| > 1 \Rightarrow \text{instability.}$$

Suppose $\det \Phi_1 < 0$; then

$$[\varepsilon^2\{(\tfrac{1}{2}\mathrm{tr}\Phi_1)^2 - \det \Phi_1\} + o(\varepsilon^2)]^{\frac{1}{2}} > |\tfrac{1}{2}(\mathrm{tr}\Phi_1)\varepsilon|$$

(a) n even: λ has two values, as we take $\pm$ the radical. $\varepsilon\, \mathrm{tr}\,\Phi_1 > 0 \Rightarrow |\lambda_1| > 1$ and $|\lambda_2| < 1$. This case is referred to as directly unstable by Loud [12].

$$\varepsilon\, \mathrm{tr}\Phi_1 < 0 \Rightarrow \text{same result.}$$

(b) n odd: again λ has two values.

$\varepsilon\, \mathrm{tr}\,\Phi_1 > 0 \Rightarrow |\lambda_1| < 1$ and $|\lambda_2| > 1 \Rightarrow$ direct instability

$\varepsilon\, \mathrm{tr}\,\Phi_1 < 0 \Rightarrow$ same result.

2.8. <u>An example</u>. In (1.1) let

$$g(x,K(t)) = \alpha\left(1 - \frac{x}{K(t)}\right)$$

$$p(x) = \beta x/(1+kx)$$

$$K(t) = K_0 + \varepsilon \cos t, \quad \alpha,\beta,k,K_0 > 0.$$

Then

$$p_x(x) = \beta/(1 + kx)^2$$

$$p_{xx}(x) = -2\beta k/(1 + kx)^3$$

$$H(x,K) = g(x,K) + xg_x(x,K) - xg(x,K)p_x(x)/p(x)$$

$$= \alpha\left(1 - \frac{2x}{K}\right) - \alpha\left(1 - \frac{x}{K}\right)\left(\frac{1}{1 + kx}\right)$$

$$H_x(x,K) = -\frac{2\alpha}{K} + \frac{\alpha(1+kK)}{K(1+kx)^2}$$

$$H_K(x,K) = \frac{\alpha x}{K^2}\left(\frac{1+2kx}{1+kx}\right).$$

We consider the equilibrium (a,b) for $\varepsilon = 0$, and we wish to solve for a and b in terms of the given positive numbers α, β, k, K_0. Since we are interested in the first quadrant only, $g(x,K)$, $p(x)$ are defined for all $x \geq 0$.

Now

$$g(0,K) = \alpha > 0, \quad g(K,K) = 0, \quad g_x(x,K) = \frac{-\alpha}{K} < 0$$

$$g_K(x,K) = \frac{\alpha x}{K^2} \geq 0, \quad g_{xK}(x,K) = \frac{\alpha}{K^2} > 0 .$$

At (a,b) we require that

(2.37) $\quad p(a) = s/c$ and $b = ag(a,K_0)/p(a)$

i.e. $\quad \frac{\beta a}{1+ka} = \frac{s}{c}$, or

(2.38) $\quad a = s/(\beta c - ks), \quad \beta c \neq ks.$

Thus $a > 0$ provided $\beta/k > s/c$.

$$\therefore \quad b = \frac{a\alpha c}{sK_0}(K_0 - a),$$

so $b > 0$ if $a < K_0$. Using (2.38),

$$b = \frac{\alpha c}{K_0(\beta c - ks)}\left(K_0 - \frac{s}{\beta c - ks}\right)$$

so we have the same restriction as before, viz. $\beta/k > s/c$.

The predator isocline is the line $x = a$, whereas the prey isocline is the curve $y = xg(x,K)/p(x)$ (see §1.5)

i.e.

$$y = \frac{\alpha}{\beta}\left(1 - \frac{x}{K}\right)(1 + kx)$$

which is a parabola.

$$y_x = \frac{\alpha}{\beta}\left\{-\frac{1}{K}(1+kx) + \left(1 - \frac{x}{K}\right)k\right\} = H(x,K)/p(x).$$

Putting $y_x = 0$ we obtain

$$x_0 = \frac{1}{2}\left(K - \frac{1}{k}\right)$$

as the abscissa of the parabola's maximum point. This implies that $H(x_0,K) = 0$.

If $x_0 < 0$, i.e. $K < 1/k$, line $x = a$ crosses the isocline to the right of the maximum point, for all $a > 0$: here $y_x < 0$ and, since $y_x\big|_{x=a} = H(a,K_0)/p(a)$, we have $H(a,K_0) < 0$, giving stability of equilibrium.

Suppose $x_0 > 0$, i.e. $K > 1/k$. Then we can have

(i) $a < \frac{1}{2}\left(K - \frac{1}{k}\right) \Rightarrow y_x\big|_{x=a} = H_0/p > 0$ (instability)

(ii) $a = \frac{1}{2}\left(K - \frac{1}{k}\right) \Rightarrow y_x\big|_{x=a} = H_0/p = 0$ (critical case)

(iii) $a > \frac{1}{2}\left(K - \frac{1}{k}\right) \Rightarrow y_x\big|_{x=a} = H_0/p < 0$ (asymptotic stability)

Now $H(x,K) = \alpha\left\{1 - \frac{2x}{K} - \frac{K - x}{K(1+kx)}\right\}$.

We wish to compare H_0^2 with $4bcpp_x$: to do this, we first consider $H^2(x,K)$ and $4bcp(x)p_x(x)$, i.e.

$$(2.39)\qquad \alpha^2\left\{1 - \frac{2x}{K} - \frac{K-x}{K(1+kx)}\right\}^2 \sim \frac{4\alpha c^2 a}{sK_0}(K_0 - a)\frac{\beta^2 x}{(1+kx)^3}.$$

At the vertex of the prey isocline, $H(x_0,K) = 0$ so that $H^2(x_0,K) < 4bcp(x_0)p_x(x_0)$, since b, c, p, p_x are all positive. By continuity, this inequality is not altered if $H^2(x,K)$ is slightly greater than zero. Hence, for some value $x = a$ (different from x_0), we have $H_0^2 < 4bcpp_x$ provided $|H_0|$ is sufficiently small; so cases III and IV can occur.

Since the right-hand side of (2.39) is a function of α, whereas the left-hand side is a function of α^2, we can choose α sufficiently large ($\alpha > 1$) so as to have, at $x = a$, $H_0^2 > 4bcpp_x$, and so case I is possible. But then we can, by continuity, pick a value for α such that $H_0^2 = 4bcpp_x$, giving rise to case II.

Hence all four cases are possible for this example if we choose suitable values for the given constants α, β, k, K_0.

We work out case I in some detail: Now

$$\begin{pmatrix} u_0(t) \\ v_0(t) \end{pmatrix}' = \begin{pmatrix} H(a,K_0) & -p(a) \\ bcp_x(a) & 0 \end{pmatrix}\begin{pmatrix} u_0(t) \\ v_0(t) \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} u_0(0) \\ v_0(0) \end{pmatrix} = \begin{pmatrix} 1 \\ 0 \end{pmatrix}$$

gives $\begin{pmatrix} u_0(t) \\ v_0(t) \end{pmatrix} = e^{tB}\begin{pmatrix} 1 \\ 0 \end{pmatrix}$ as a solution (see [1] chap. 3) where

$$B = \begin{pmatrix} H(a,K_0) & -p(a) \\ bcp_x(a) & 0 \end{pmatrix}$$

$$e^{tB} = \begin{pmatrix} x_\xi & x_\eta \\ y_\xi & y_\eta \end{pmatrix}.$$

Hence

$$(2.40a)\qquad \begin{pmatrix} u_0(t) \\ v_0(t) \end{pmatrix} = \begin{pmatrix} x_\xi \\ y_\xi \end{pmatrix} = \frac{1}{(H_0^2 - 4bcpp_x)^{\frac{1}{2}}}\begin{pmatrix} \rho_1 e^{\rho_1 t} - \rho_2 e^{\rho_2 t} \\ bcp_x(e^{\rho_1 t} - e^{\rho_2 t}) \end{pmatrix}.$$

With the i.c.'s $\begin{pmatrix} u_0(0) \\ v_0(0) \end{pmatrix} = \begin{pmatrix} 0 \\ 1 \end{pmatrix}$ we obtain

$$(2.40b) \qquad \begin{pmatrix} u_0(t) \\ v_0(t) \end{pmatrix} = \begin{pmatrix} x_\eta \\ y_\eta \end{pmatrix} = \frac{1}{(H_0^2 - 4bcpp_x)^{\frac{1}{2}}} \begin{pmatrix} p(e^{\rho_2 t} - e^{\rho_1 t} \\ \rho_1 e^{\rho_2 t} - \rho_2 e^{\rho_1 t} \end{pmatrix}$$

We recall (2.35)

$$(2.35) \qquad \begin{pmatrix} u_1(t) \\ v_1(t) \end{pmatrix} = e^{tB} \int_0^t e^{-rB} f(r)dr$$

where

$$f(r) = \begin{pmatrix} H_x(a,K_0)\phi_1(r)+H_K(a,K_0)\cos r & -p_x(a)\phi_1(r) \\ c\psi p_{xx}(a)\phi_1(r) + cp_x(a)\psi_1(r) & cp_x(a)\phi_1(r) \end{pmatrix} \begin{pmatrix} u_0(r) \\ v_0(r) \end{pmatrix}$$

$$(2.41) \quad f(r) = \begin{pmatrix} -\frac{2\alpha}{K_0}\phi_1(r) + \frac{\alpha(1+kK_0)}{K_0(1+ka)^2}\phi_1(r) + \frac{\alpha a}{K_0^2}\left(\frac{1+2ka}{1+ka}\right)\cos r & \frac{-\beta\phi_1(r)}{(1+ka)^2} \\ \frac{-2c\beta k}{(1+ka)^3}\psi\phi_1(r) + \frac{c\beta\psi_1(r)}{(1+ka)^2} & \frac{c\beta\phi_1(r)}{(1+ka)^2} \end{pmatrix} \begin{pmatrix} u_0(r) \\ v_0(r) \end{pmatrix}.$$

Now $\phi_1(t) = \frac{\partial}{\partial\varepsilon}\phi(t,\varepsilon)\Big|_{\varepsilon=0} = \frac{\partial}{\partial\varepsilon}x(t,\xi,\eta,\varepsilon)\Big|_{\varepsilon=0}$. Hence

$$(2.42a) \qquad \phi_1(t) = x_\xi\xi_\varepsilon + x_\eta\eta_\varepsilon + x_\varepsilon.$$

Similarly,

$$(2.42b) \qquad \psi_1(t) = y_\xi\xi_\varepsilon + y_\eta\eta_\varepsilon + y_\varepsilon.$$

Hence

$$\phi_1(t) = \frac{(\rho_1 e^{\rho_1 t} - \rho_2 e^{\rho_2 t})\xi_\varepsilon + p(e^{\rho_2 t} - e^{\rho_1 t})\eta_\varepsilon}{(H_0^2 - 4bcpp_x)^{\frac{1}{2}}} + x_\varepsilon$$

$$\psi_1(t) = \frac{bcp_x(e^{\rho_1 t} - e^{\rho_2 t})\xi_\varepsilon + (\rho_1 e^{\rho_2 t} - \rho_2 e^{\rho_1 t})\eta_\varepsilon}{(H_0^2 - 4bcpp_x)^{\frac{1}{2}}} + y_\varepsilon$$

where

$$\rho_1,\rho_2 = \frac{1}{2}(H_0^2 \pm \sqrt{H_0^2 - 4bcpp_x}).$$

From (2.11),

$$\begin{pmatrix} x_\varepsilon(t,0,0,0) \\ y_\varepsilon(t,0,0,0) \end{pmatrix} = ag_K(a,K_0)e^{tB}\int_0^t e^{-rH_0}\cos r \begin{pmatrix} y_\eta(r) \\ -y_\xi(r) \end{pmatrix} dr$$

$$= \frac{ag_K(a,K_0)e^{tB}}{(H_0^2-4bcpp_x)^{\frac{1}{2}}}\int_0^t e^{-rH_0}\cos r \begin{pmatrix} \rho_1 e^{\rho_2 r} - \rho_2 e^{\rho_1 r} \\ bcp_x(e^{\rho_2 r} - e^{\rho_1 r}) \end{pmatrix} dr$$

$$= \frac{ag_K(a,K_0)e^{tB}}{(H_0^2-4bcpp_x)^{\frac{1}{2}}}\int_0^t \begin{pmatrix} \rho_1 e^{-\rho_1 r} - \rho_2 e^{-\rho_2 r} \\ bcp_x(e^{-\rho_1 r} - e^{-\rho_2 r}) \end{pmatrix} \cos r\, dr$$

since $\rho_1 + \rho_2 = H_0$. Now

$$\int_0^t e^{-\rho_1 r}\cos r\, dr = e^{-\rho_1 r}\sin r\Big|_0^t + \rho_1\int_0^t e^{-\rho_1 r}\sin r\, dr$$

$$= e^{-\rho_1 t}\sin t - \rho_1 e^{-\rho_1 t}\cos t + \rho_1 - \rho_1^2\int_0^t e^{-\rho_1 r}\cos r\, dr$$

$$\Rightarrow \int_0^t e^{-\rho_1 r}\cos r\, dr = \frac{1}{1+\rho_1^2}\left\{e^{-\rho_1 t}(\sin t - \rho_1\cos t) + \rho_1\right\}.$$

Hence

$$\begin{pmatrix} x_\varepsilon \\ y_\varepsilon \end{pmatrix} = \frac{ag_K(a,K_0)}{(H_0^2-4bcpp_x)^{\frac{1}{2}}}\begin{pmatrix} x_\xi & x_\eta \\ y_\xi & y_\eta \end{pmatrix}\cdot$$

$$\cdot \begin{pmatrix} \frac{\rho_1}{1+\rho_1^2}\left\{e^{-\rho_1 t}(\sin t - \rho_1\cos t) + \rho_1\right\} - \frac{\rho_2}{1+\rho_2^2}\left\{e^{-\rho_2 t}(\sin t - \rho_2\cos t) + \rho_2\right\} \\ \frac{bcp_x}{1+\rho_1^2}\left\{e^{-\rho_1 t}(\sin t - \rho_1\cos t) + \rho_1\right\} - \frac{bcp_x}{1+\rho_2^2}\left\{e^{-\rho_2 t}(\sin t - \rho_2\cos t) + \rho_2\right\} \end{pmatrix}$$

$$= \frac{ag_K(a,K_0)}{H_0^2-4bcpp_x}\begin{pmatrix} \rho_1 e^{\rho_1 t} - \rho_2 e^{\rho_2 t} & p(e^{\rho_2 t} - e^{\rho_1 t}) \\ bcp_x(e^{\rho_1 t} - e^{\rho_2 t}) & \rho_1 e^{\rho_2 t} - \rho_2 e^{\rho_1 t} \end{pmatrix}\cdot$$

$$\cdot \begin{pmatrix} \dfrac{\rho_1\{e^{-\rho_1 t}(\sin t - \rho_1 \cos t) + \rho_1\}}{1+\rho_1^2} - \dfrac{\rho_2\{e^{-\rho_2 t}(\sin t - \rho_2 \cos t) + \rho_2\}}{1+\rho_2^2} \\ \dfrac{bcp_x\{e^{-\rho_1 t}(\sin t - \rho_1 \cos t) + \rho_1\}}{1+\rho_1^2} - \dfrac{bcp_x\{e^{-\rho_2 t}(\sin t - \rho_2 \cos t) + \rho_2\}}{1+\rho_2^2} \end{pmatrix}$$

$$= C(\rho_1-\rho_2) \begin{pmatrix} \dfrac{\rho_1}{1+\rho_1^2}(\sin t - \rho_1 \cos t + \rho_1 e^{\rho_1 t}) - \dfrac{\rho_2}{1+\rho_2^2}(\sin t - \rho_2 \cos t + \rho_2 e^{\rho_2 t}) \\ bcp_x\left(\dfrac{\sin t - \rho_1 \cos t + \rho_1 e^{\rho_1 t}}{1+\rho_1^2} - \dfrac{\sin t - \rho_2 \cos t + \rho_2 e^{\rho_2 t}}{1+\rho_2^2}\right) \end{pmatrix}$$

since $bcpp_x = \rho_1\rho_2$, where $C = \dfrac{ag_K(a,K_0)}{H_0^2 - 4bcpp_x}$

$$= \frac{C(\rho_1-\rho_2)}{(1+\rho_1^2)(1+\rho_2^2)} \cdot$$

$$\cdot \begin{pmatrix} (\rho_1-\rho_2)(1-\rho_1\rho_2)\sin t - (\rho_1^2-\rho_2^2)\cos t + (\rho_1^2+\rho_1^2\rho_2^2)e^{\rho_1 t} - (\rho_2^2+\rho_1^2\rho_2^2)e^{\rho_2 t} \\ bcp_x\{-(\rho_1^2-\rho_2^2)\sin t - (\rho_1-\rho_2)(1-\rho_1\rho_2)\cos t + (\rho_1+\rho_1\rho_2^2)e^{\rho_1 t} - (\rho_2+\rho_1^2\rho_2)e^{\rho_1 t}\} \end{pmatrix}$$

$$(2.43) \quad \begin{pmatrix} x_\varepsilon \\ y_\varepsilon \end{pmatrix} = C_1(\rho_1-\rho_2) \begin{pmatrix} (1-\rho_1\rho_2)\sin t - (\rho_1+\rho_2)\cos t \\ bcp_x\{-(\rho_1+\rho_2)\sin t - (1-\rho_1\rho_2)\cos t \end{pmatrix} +$$

$$+ C_1(\rho_1+\rho_1\rho_2^2)\begin{pmatrix} \rho_1 \\ bcp_x \end{pmatrix} e^{\rho_1 t} - C_1(\rho_2+\rho_1^2\rho_2)\begin{pmatrix} \rho_2 \\ bcp_x \end{pmatrix} e^{\rho_2 t}$$

where $C_1 = C(\rho_1-\rho_2)/(1+\rho_1^2)(1+\rho_2^2)$.

From (2.42)

$$\begin{pmatrix} \phi_1(t) \\ \psi_1(t) \end{pmatrix} = \begin{pmatrix} x_\xi & x_\eta \\ y_\xi & y_\eta \end{pmatrix} \begin{pmatrix} \xi_\varepsilon(0) \\ \eta_\varepsilon(0) \end{pmatrix} + \begin{pmatrix} x_\varepsilon \\ y_\varepsilon \end{pmatrix} .$$

But, from (2.30),

$$\begin{pmatrix} \xi_\varepsilon(0) \\ \eta_\varepsilon(0) \end{pmatrix} = -J^{-1}\begin{pmatrix} x_\varepsilon \\ y_\varepsilon \end{pmatrix} .$$

Hence, from (2.42)

$$\begin{pmatrix} \phi_1(t) \\ \psi_1(t) \end{pmatrix} = -\begin{pmatrix} x_\xi & x_\eta \\ y_\xi & y_\eta \end{pmatrix} J^{-1}\begin{pmatrix} x_\varepsilon \\ y_\varepsilon \end{pmatrix} + \begin{pmatrix} x_\varepsilon \\ y_\varepsilon \end{pmatrix}$$

$$= \left[I - \begin{pmatrix} x_\xi & x_\eta \\ y_\xi & y_\eta \end{pmatrix} J^{-1} \right]\begin{pmatrix} x_\varepsilon \\ y_\varepsilon \end{pmatrix} .$$

Using (2.43) and the values of x_ξ, y_ξ, x_η, y_η given by (2.5)-(2.8) we can determine the value of $(\phi_1(t),\psi_1(t))$; these can then be inserted into (2.41) in order to find $f(r)$ and, once this is computed, we can use (2.35) to evaluate $(u_1(t), v_1(t))$. We then substitute this, together with (2.40) into (2.33) in order to find u and v, the required solutions to problem (2.32) up to order ε.

The other cases follow the same pattern of computations.

CHAPTER III

Proceeding from the assumption that the equilibrium corresponding to the autonomous system is unstable we saw in Chapter I that this gave rise to the existence of a stable limit cycle.

In what follows we concentrate on the nonautonomous system and consider the possibility for the existence of a perturbed stable limit cycle. This leads us, in a natural way, into applications of critical cases of the Implicit Function Theorem, as set out in Freedman [4].

3.1. Existence of a perturbed periodic solution. Suppose for $\varepsilon = 0$ there exists a non-trivial periodic solution $x = \phi_0(t)$, $y = \psi_0(t)$ of the system

$$x' = xg(x,K) - yp(x) \tag{3.1a}$$

$$y' = y\big(-s + cp(x)\big) \tag{3.1b}$$

$$K = K_0 + \varepsilon\kappa(t)$$

with critical point at (a,b). Note that (3.1) is autonomous for $\varepsilon = 0$.

Assume $H(a,K_0) > 0$ so that there exists an unstable solution at (a,b) and suppose $\big(\phi_0(t),\psi_0(t)\big)$ is a limit cycle of period ω, $\kappa(t+\omega) = \kappa(t)$; let $\phi_0(0) = a + A$, $(A > 0)$ $\psi_0(0) = b$.

Note that, in general, it would be highly unlikely that the limit cycle of the system should have the same period as the external forcing term. However, in the biological case under consideration, it seems plausible that this should be so if we assume, for instance, that both the unperturbed eventual predator-prey populations and the carrying

capacity have seasonal fluctuations of period one year.

Let $x(t,\xi,\eta,\varepsilon)$, $y(t,\xi,\eta,\varepsilon)$ be a solution of (3.1) such that

$$x(0,\xi,\eta,\varepsilon) = a + A + \xi$$

$$y(0,\xi,\eta,\varepsilon) = b + \eta.$$

System (3.1) is now nonautonomous and we can write (cf. (2.1))

(3.2a) $$F(\xi,\eta,\varepsilon) = x(\omega,\xi,\eta,\varepsilon) - a - A - \xi$$

(3.2b) $$G(\xi,\eta,\varepsilon) = y(\omega,\xi,\eta,\varepsilon) - b - \eta.$$

We need to solve $F(\xi,\eta,\varepsilon) = G(\xi,\eta,\varepsilon) = 0$ in order to obtain a periodic solution.

Since $x(t,0,0,0) = \phi_0(t)$ and $y(t,0,0,0) = \psi_0(t)$

$$F(0,0,0) = x(\omega,0,0,0) - a - A = 0$$

$$G(0,0,0) = y(\omega,0,0,0) - b = 0.$$

3.2. Variational system. The variational equations for (3.1) with respect to $\phi_0(t)$, $\psi_0(t)$ are (cf. [1] chap. 13)

(3.3a) $$u' = H(\phi_0(t),K_0)u - p(\phi_0(t))v$$

(3.3b) $$v' = c\psi_0(t)p_x(\phi_0(t))u + (-s + cp(\phi_0(t)))v$$

This system varies from (2.2) in that the coefficients are non-constant. Since $(\phi_0(t), \psi_0(t))$ is a solution of (3.1) it follows that $(\phi_0'(t), \psi_0'(t))$ is a solution of the variational system (3.3) (see [1] chap. 13 and Loud [13], part I).

Now $$\phi_0'(0) = \phi_0\, g(\phi_0,K_0) - \psi_0\, p(\phi_0) = (a+A)g(a+A,K_0) - bp(a+A) < 0$$

$$\psi_0'(0) = \psi_0(-s + cp(\phi_0)) = b(-s + cp(a+A)) > 0.$$

Hence we let

(3.4) $\phi_0'(0) = \alpha < 0$ and $\psi_0'(0) = \beta > 0$.

Suppose $(q_1(t), q_2(t))$ is another independent solution of (3.3) and choose $q_1(0) = 1$, $q_2(0) = 0$; since $(\alpha,\beta) \neq (1,0)$ it is clear that (q_1,q_2), (ϕ_0',ψ_0') are independent solutions. Now

(3.5a) $F_\xi(0,0,0) = x_\xi(\omega,0,0,0) - 1, \quad x_\xi(0) = 1$

(3.5b) $G_\xi(0,0,0) = y_\xi(\omega,0,0,0), \quad y_\xi(0) = 0$

(3.5c) $F_\eta(0,0,0) = x_\eta(\omega,0,0,0), \quad x_\eta(0) = 0$

(3.5d) $G_\eta(0,0,0) = y_\eta(\omega,0,0,0) - 1, \quad y_\eta(0) = 1.$

Since $(q_1(t), q_2(t))$ and $(\phi_0'(t), \psi_0'(t))$ are linearly independent solutions of (3.3) we have, for any solution (x_ξ,y_ξ)

$$\begin{pmatrix} x_\xi(t,0,0,0) \\ y_\xi(t,0,0,0) \end{pmatrix} = c_0 \begin{pmatrix} \phi_0'(t) \\ \psi_0'(t) \end{pmatrix} + c_1 \begin{pmatrix} q_1(t) \\ q_2(t) \end{pmatrix}, \quad c_0, c_1 \text{ constants.}$$

At $t = 0$, $\begin{pmatrix} 1 \\ 0 \end{pmatrix} = c_0 \begin{pmatrix} \alpha \\ \beta \end{pmatrix} + c_1 \begin{pmatrix} 1 \\ 0 \end{pmatrix} \Rightarrow c_0 = 0, \quad c_1 = 1$

(3.6) $\therefore \quad x_\xi(t,0,0,0) = q_1(t), \quad y_\xi(t,0,0,0) = q_2(t).$

Also

$$\begin{pmatrix} x_\eta(t,0,0,0) \\ y_\eta(t,0,0,0) \end{pmatrix} = d_0 \begin{pmatrix} \phi_0'(t) \\ \psi_0'(t) \end{pmatrix} + d_1 \begin{pmatrix} q_1(t) \\ q_2(t) \end{pmatrix}, \quad d_0, d_1 \text{ constants.}$$

At $t = 0$, $\begin{pmatrix} 0 \\ 1 \end{pmatrix} = d_0 \begin{pmatrix} \alpha \\ \beta \end{pmatrix} + d_1 \begin{pmatrix} 1 \\ 0 \end{pmatrix} \Rightarrow d_0 = \frac{1}{\beta}, \quad d_1 = -\frac{\alpha}{\beta}$

(3.7a) $\therefore \quad x_\eta(t,0,0,0) = \frac{1}{\beta}\{\phi_0'(t) - \alpha q_1(t)\}$

(3.7b) $\quad y_\eta(t,0,0,0) = \frac{1}{\beta}\{\psi_0'(t) - \alpha q_2(t)\}.$

Hence

$$J = \begin{pmatrix} x_\xi - 1 & x_\eta \\ y_\xi & y_\eta - 1 \end{pmatrix}$$

$$= \begin{pmatrix} q_1(\omega) - 1 & -\frac{\alpha}{\beta}(q_1(\omega) - 1) \\ q_2(\omega) & -\frac{\alpha}{\beta} q_2(\omega) \end{pmatrix}$$

and so $\det J = 0$.

This implies that we cannot directly use the Implicit Function Theorem to solve for ξ, η as functions of ε so that we must consider critical cases, as given in Freedman [4].

We are unable at this stage to formulate values for $q_1(t)$, $q_2(t)$, but proceed on the assumption that $q_2(\omega) \neq 0$: this is supported by results in Freedman and Waltman [8], and also by the work of Loud [12].

3.3. Existence of solutions with $\det J = 0$. With the crucial assumption $q_2(\omega) \neq 0$ we have, using (3.6) and (3.5b), that

$$G_\xi(0,0,0) \neq 0, \quad G(0,0,0) = 0$$

and we can apply the Implicit Function Theorem (see [4]) to obtain ξ as a function of η, ε, viz, there exists a unique $\xi(\eta,\varepsilon)$, $\xi(0,0) = 0$ such that

(3.8) $\quad G\big(\xi(\eta,\varepsilon),\eta,\varepsilon\big) = 0$ with η, ε independent.

Hence

(3.9) $\quad G_\xi \xi_\eta + G_\eta = G_\xi \xi_\varepsilon + G_\varepsilon = 0,$

so that

$$\xi_\eta = -G_\eta/G_\xi, \qquad \xi_\varepsilon = -G_\varepsilon/G_\xi .$$

Then

$$\xi(\eta,\varepsilon) = \xi(0,0) + \left(\eta\frac{\partial}{\partial\eta} + \varepsilon\frac{\partial}{\partial\varepsilon}\right)\xi(0,0) + o(\eta,\varepsilon)$$

$$\Rightarrow \quad \xi(\eta,\varepsilon) = -\eta\frac{G_\eta(0,0,0)}{G_\xi(0,0,0)} - \varepsilon\frac{G_\varepsilon(0,0,0)}{G_\xi(0,0,0)} + o(\eta,\varepsilon).$$

We now wish to obtain η as a function of ε. To do this we need to find $F_\varepsilon(0,0,0)$, $G_\varepsilon(0,0,0)$. From (3.2)

$$F_\varepsilon(0,0,0) = x_\varepsilon(\omega,0,0,0), \qquad x_\varepsilon(0) = 0$$

$$G_\varepsilon(0,0,0) = y_\varepsilon(\omega,0,0,0), \qquad y_\varepsilon(0) = 0$$

At $\xi = \eta = \varepsilon = 0$, x_ε, y_ε satisfy the variational system

$$x_\varepsilon' = H\big(\phi_0(t),K_0\big)x_\varepsilon - p\big(\phi_0(t)\big)y_\varepsilon + \phi_0(t)g_K\big(\phi_0(t),K_0\big)\kappa(t)$$

$$y_\varepsilon' = c\psi_0(t)p_x\big(\phi_0(t)\big)x_\varepsilon + \big(-s + cp\big(\phi_0(t)\big)\big)y_\varepsilon$$

and so (see [1] chap. 3),

$$(3.10) \qquad \begin{pmatrix} x_\varepsilon(t,0,0,0) \\ y_\varepsilon(t,0,0,0) \end{pmatrix} = \Phi(t)\int_0^t \Phi^{-1}(r)\begin{pmatrix} \phi_0(r)g_K\big(\phi_0(r),K_0\big)\kappa(r) \\ 0 \end{pmatrix} dr$$

where $\Phi(t) = \begin{pmatrix} q_1(t) & \phi_0'(t) \\ q_2(t) & \psi_0'(t) \end{pmatrix}$ is a fundamental matrix for (3.3).

Hence

$$(3.11) \qquad \begin{pmatrix} F_\varepsilon(0,0,0) \\ G_\varepsilon(0,0,0) \end{pmatrix} = \Phi(\omega)\int_0^\omega \Phi^{-1}(t)\begin{pmatrix} \phi_0(t)g_K\big(\phi_0(t),K_0\big)\kappa(t) \\ 0 \end{pmatrix} dt.$$

Having $G\big(\xi(\eta,\varepsilon),\eta,\varepsilon\big) = 0$, $\xi(0,0) = 0$ we let

$$(3.12) \qquad D(\eta,\varepsilon) = F\big(\xi(\eta,\varepsilon),\eta,\varepsilon\big).$$

Thus

$$D(0,0) = F(0,0,0) = 0$$

$$D_\eta(0,0) = F_\xi(0,0,0)\xi_\eta(0,0) + F_\eta(0,0,0)$$

$$= [q_1(\omega)-1]\left[-\frac{G_\eta(0,0,0)}{G_\xi(0,0,0)} - \frac{\alpha}{\beta}\right]$$

$$= 0, \quad \text{using (3.4), (3.5), (3.6), (3.7), (3.9).}$$

$$D_\varepsilon(0,0) = F_\xi(0,0,0)\xi_\varepsilon(0,0) + F_\varepsilon(0,0,0)$$

$$= \left(1 - q_1(\omega)\right)\frac{G_\varepsilon(0,0,0)}{q_2(\omega)} + F_\varepsilon(0,0,0), \quad \text{using (3.5), (3.6), (3.9),}$$

where $F_\varepsilon(0,0,0)$, $G_\varepsilon(0,0,0)$ are given by (3.11).

If $D_\varepsilon(0,0) = 0$ we let $\eta = \gamma\varepsilon$ and, by applying case II of the Implicit Function Theorem (see [4]), we can express γ as a function of ε, so eventually obtaining η as a function of ε, as required. If $D_\varepsilon(0,0) \neq 0$, then we apply case III of paper [4] to obtain $\eta(\varepsilon)$.

However, in order to apply these critical cases of the Implicit Function Theorem, we need to compute $D_{\eta\eta}(0,0)$, $D_{\eta\varepsilon}(0,0)$, $D_{\varepsilon\varepsilon}(0,0)$.

From (3.12)

$$(3.13)\quad D_{\eta\eta}(0,0) = F_{\xi\xi}(0,0,0)\xi_\eta^2(0,0) + 2F_{\xi\eta}(0,0,0)\xi_\eta(0,0) + F_{\eta\eta}(0,0,0) + F_\xi(0,0,0)\xi_{\eta\eta}(0,0)$$

$$(3.14)\quad D_{\eta\varepsilon}(0,0) = F_{\xi\xi}(0,0,0)\xi_\eta(0,0)\xi_\varepsilon(0,0) + F_{\xi\eta}(0,0,0)\xi_\varepsilon(0,0) + F_{\xi\varepsilon}(0,0,0)\xi_\eta(0,0) + F_{\eta\varepsilon}(0,0,0) + F_\xi(0,0,0)\xi_{\eta\varepsilon}(0,0)$$

$$(3.15)\quad D_{\varepsilon\varepsilon}(0,0) = F_{\xi\xi}(0,0,0)\xi_\varepsilon^2(0,0) + 2F_{\xi\varepsilon}(0,0,0)\xi_\varepsilon(0,0) + F_{\varepsilon\varepsilon}(0,0,0) + F_\xi(0,0,0)\xi_{\varepsilon\varepsilon}(0,0).$$

We proceed to derive the second partial derivatives of F, G and ξ required in the above expressions:

From (3.5),

$$F_{\xi\xi}(0,0,0) = x_{\xi\xi}(\omega,0,0,0), \quad G_{\xi\xi}(0,0,0) = y_{\xi\xi}(\omega,0,0,0) .$$

From (3.1), x_ξ, y_ξ satisfy the variational system,

$$x'_\xi = H(x,K)x_\xi - p(x)y_\xi, \quad x_\xi(0) = 1 \tag{3.16a}$$

$$y'_\xi = cyp_x(x)x_\xi + \left(-s + cp(x)\right)y_\xi, \quad y_\xi(0) = 0. \tag{3.16b}$$

Hence, at $\xi = \eta = \varepsilon = 0$, we have

$$x'_{\xi\xi} = H\left(\phi_0(t),K_0\right)x_{\xi\xi} - p\left(\phi_0(t)\right)y_{\xi\xi} + H_x\left(\phi_0(t),K_0\right)x_\xi^2 - p_x\left(\phi_0(t)\right)x_\xi y_\xi$$

$$y'_{\xi\xi} = c\psi_0(t)p_x\left(\phi_0(t)\right)x_{\xi\xi} + \left[-s + cp\left(\phi_0(t)\right)\right]y_{\xi\xi} + c\psi_0(t)p_{xx}\left(\phi_0(t)\right)x_\xi^2 + \\ + 2cp_x\left(\phi_0(t)\right)x_\xi y_\xi$$

$$x_{\xi\xi}(0) = y_{\xi\xi}(0) = 0.$$

Thus (see [1] chap. 3)

$$\begin{pmatrix} x_{\xi\xi}(t,0,0,0) \\ y_{\xi\xi}(t,0,0,0) \end{pmatrix} = \Phi(t)\int_0^t \Phi^{-1}(r)\begin{pmatrix} H_x\left(\phi_0(r),K_0\right)x_\xi^2 - p_x\left(\phi_0(r)\right)x_\xi y_\xi \\ c\psi_0(r)p_{xx}\left(\phi_0(t)\right)x_\xi^2 + 2cp_x\left(\phi_0(r)\right)x_\xi y_\xi \end{pmatrix} dr$$

$$\begin{pmatrix} x_{\xi\xi}(t,0,0,0) \\ y_{\xi\xi}(t,0,0,0) \end{pmatrix} = \Phi(t)\int_0^t \Phi^{-1}(r)q_1(r) \cdot \\ \cdot \begin{pmatrix} H_x\left(\phi_0(r),K_0\right)q_1(r) - p_x\left(\phi_0(r)\right)q_2(r) \\ c\psi_0(r)p_{xx}\left(\phi_0(r)\right)q_1(r) + 2cp_x\left(\phi_0(r)\right)q_2(r) \end{pmatrix} dr, \text{ using (3.6).} \tag{3.17}$$

$$\det \Phi(t) = \det \Phi(0) \exp \int_0^t \operatorname{tr} B(r)dr$$

$$= \beta \exp \int_0^t \left[H\left(\phi_0(r),K_0\right) - s + cp\left(\phi_0(r)\right)\right]dr, \text{ since}$$

$$\Phi(0) = \begin{pmatrix} 1 & \alpha \\ 0 & \beta \end{pmatrix}$$

$$\Rightarrow \det \Phi(t) \neq 0.$$

Hence $\begin{pmatrix} F_{\xi\xi}(0,0,0) \\ G_{\xi\xi}(0,0,0) \end{pmatrix}$ is given by (3.17) with t replaced by ω.

From (3.5)

$$F_{\xi\eta}(0,0,0) = x_{\xi\eta}(\omega,0,0,0), \quad G_{\xi\eta}(0,0,0) = y_{\xi\eta}(\omega,0,0,0).$$

Differentiating (3.16) with regard to η and putting $\xi = \eta = \varepsilon = 0$

$$x'_{\xi\eta} = H(\phi_0(t),K_0)x_{\xi\eta} - p(\phi_0(t))y_{\xi\eta} + H_x(\phi_0(t),K_0)x_\xi x_\eta - p_x(\phi_0(t))x_\eta y_\xi$$

$$y'_{\xi\eta} = c\psi_0(t)p_x(\phi_0(t))x_{\xi\eta} + [-s+cp(\phi_0(t))]y_{\xi\eta} + c\psi_0(t)p_{xx}(\phi_0(t))x_\xi x_\eta +$$
$$+ cp_x(\phi_0(t))x_\xi y_\eta + cp_x(\phi_0(t))x_\eta y_\xi.$$

$$x_{\xi\eta}(0) = y_{\xi\eta}(0) = 0.$$

Hence

$$\begin{pmatrix} x_{\xi\eta}(t,0,0,0) \\ y_{\xi\eta}(t,0,0,0) \end{pmatrix} = \Phi(t)\int_0^t \Phi^{-1}(r) \begin{pmatrix} H_x(\phi_0(r),K_0)x_\xi x_\eta - p_x(\phi_0(r))x_\eta y_\xi \\ c\psi_0(r)p_{xx}(\phi_0(r))x_\xi x_\eta + cp_x(\phi_0(r))(x_\xi y_\eta + x_\eta y_\xi) \end{pmatrix} dr$$

and

$$(3.18) \quad \begin{pmatrix} F_{\xi\eta}(0,0,0) \\ G_{\xi\eta}(0,0,0) \end{pmatrix} = \frac{\Phi(\omega)}{\beta}\int_0^\omega \Phi^{-1}(t) \cdot$$

$$\cdot \begin{pmatrix} H_x(\phi_0(t),K_0)q_1(t)(\phi_0'(t) - \alpha q_1(t)) - p_x(\phi_0(t))q_2(t)(\phi_0'(t) - \alpha q_1(t)) \\ c\psi_0(t)p_{xx}(\phi_0(t))q_1(t)(\phi_0'(t) - \alpha q_1(t)) + cp_x(\phi_0(t))[q_1(t)(\psi_0'(t) - \alpha q_2(t)) \\ \qquad + q_2(t)(\phi_0'(t) - \alpha q_1(t))] \end{pmatrix} dt$$

using (3.6), (3.7)

From (3.16), with $\xi = \eta = \varepsilon = 0$,

$$x'_{\xi\varepsilon} = H(\phi_0(t),K_0)x_{\xi\varepsilon} - p(\phi_0(t))y_{\xi\varepsilon} + H_x(\phi_0(t),K_0)x_\xi x_\varepsilon + H_K(\phi_0(t),K_0)\kappa(t)x_\xi - \\ - p_x(\phi_0(t))x_\varepsilon y_\xi .$$

$$y'_{\xi\varepsilon} = c\psi_0(t)p_x(\phi_0(t))x_{\xi\varepsilon} + [-s+cp(\phi_0(t))]y_{\xi\varepsilon} + c\psi_0(t)p_{xx}(\phi_0(t))x_\xi x_\varepsilon + \\ + cp_x(\phi_0(t))(x_\xi y_\varepsilon + x_\varepsilon y_\xi)$$

$$x_{\xi\varepsilon}(0) = y_{\xi\varepsilon}(0) = 0.$$

Since $F_{\xi\varepsilon}(0,0,0) = x_{\xi\varepsilon}(\omega,0,0,0)$, $G_{\xi\varepsilon}(0,0,0) = y_{\xi\varepsilon}(\omega,0,0,0)$ we have

$$(3.19)\quad \begin{bmatrix} F_{\xi\varepsilon}(0,0,0) \\ G_{\xi\varepsilon}(0,0,0) \end{bmatrix} = \Phi(\omega)\int_0^\omega \Phi^{-1}(t)\cdot$$

$$\cdot \begin{bmatrix} H_x(\phi_0(t),K_0)x_\xi x_\varepsilon + H_K(\phi_0(t),K_0)\kappa(t)x_\xi - p_x(\phi_0(t))x_\varepsilon y_\xi \\ c\psi_0(t)p_{xx}(\phi_0(t))x_\xi x_\varepsilon + cp_x(\phi_0(t))(x_\xi y_\varepsilon + x_\varepsilon y_\xi) \end{bmatrix} dt$$

where x_ξ, y_ξ, x_η, y_η, x_ε, y_ε are given by (3.6), (3.7), 3.10). From (3.1)

$$(3.20a)\quad x'_\eta = H(x,K)x_\eta - p(x)y_\eta$$

$$(3.20b)\quad y'_\eta = cyp_x(x)x_\eta + (-s + cp(x))y_\eta .$$

Hence, at $\xi = \eta = \varepsilon = 0$, we have

$$x'_{\eta\eta} = H(\phi_0(t),K_0)x_{\eta\eta} - p(\phi_0(t))y_{\eta\eta} + H_x(\phi_0(t),K_0)x_\eta^2 - p_x(\phi_0(t))x_\eta y_\eta$$

$$y'_{\eta\eta} = c\psi_0(t)p_x(\phi_0(t))x_{\eta\eta} + [-s+cp(\phi_0(t))]y_{\eta\eta} + c\psi_0(t)p_{xx}(\phi_0(t))x_\eta^2 + 2cp_x(\phi_0(t))x_\eta y_\eta$$

$$x_{\eta\eta}(0) = y_{\eta\eta}(0) = 0.$$

Using (3.5) and (3.7), we arrive at

$$(3.21)\quad \begin{pmatrix} F_{\eta\eta}(0,0,0) \\ G_{\eta\eta}(0,0,0) \end{pmatrix} = \frac{\Phi(\omega)}{\beta^2} \int_0^{\omega} \phi^{-1}(t) \left(\phi_0'(t) - \alpha q_1(t)\right) \cdot$$

$$\cdot \begin{pmatrix} H_x\left(\phi_0(t),K_0\right)\left(\phi_0'(t) - \alpha q_1(t)\right) - p_x\left(\phi_0(t)\right)\left(\psi_0'(t) - \alpha q_2(t)\right) \\ c\psi_0(t) p_{xx}\left(\phi_0(t)\right)\left(\phi_0'(t) - \alpha q_1(t)\right) + 2c p_x\left(\phi_0(t)\right)\left(\psi_0'(t) - \alpha q_2(t)\right) \end{pmatrix} dt$$

From (3.20), with $\xi = \eta = \varepsilon = 0$, we have

$$x_{\eta\varepsilon}' = H\left(\phi_0(t),K_0\right)x_{\eta\varepsilon} - p\left(\phi_0(t)\right)y_{\eta\varepsilon} + H_x\left(\phi_0(t),K_0\right)x_\eta x_\varepsilon + H_K\left(\phi_0(t),K_0\right)\kappa(t)x_\eta - p_x\left(\phi_0(t)\right)x_\varepsilon y_\eta$$

$$y_{\eta\varepsilon}' = c\psi_0(t)p_x\left(\phi_0(t)\right)x_{\eta\varepsilon} + \left[-s + cp\left(\phi_0(t)\right)\right]y_{\eta\varepsilon} + c\psi_0(t)p_{xx}\left(\phi_0(t)\right)x_\eta x_\varepsilon + cp_x\left(\phi_0(t)\right)\left(x_\eta y_\varepsilon + x_\varepsilon y_\eta\right)$$

$$x_{\eta\varepsilon}(0) = y_{\eta\varepsilon}(0) = 0,$$

thus giving, after using (3.5)

$$(3.22)\quad \begin{pmatrix} F_{\eta\varepsilon}(0,0,0) \\ G_{\eta\varepsilon}(0,0,0) \end{pmatrix} = \Phi(\omega) \int_0^{\omega} \phi^{-1}(t) \cdot$$

$$\cdot \begin{pmatrix} H_x\left(\phi_0(t),K_0\right)x_\eta x_\varepsilon + H_K\left(\phi_0(t),K_0\right)\kappa(t)x_\eta - p_x\left(\phi_0(t)\right)x_\varepsilon y_\eta \\ c\psi_0(t)p_{xx}\left(\phi_0(t)\right)x_\eta x_\varepsilon + cp_x\left(\phi_0(t)\right)\left(x_\eta y_\varepsilon + x_\varepsilon y_\eta\right) \end{pmatrix} dt$$

where x_η, y_η, x_ε, y_ε are given by (3.7), (3.10).

From (3.1) we obtain

$$(3.23a)\quad x_\varepsilon' = H(x,K)x_\varepsilon - p(x)y_\varepsilon + xg_K(x,K)\kappa(t)$$

$$(3.23b)\quad y_\varepsilon' = cyp_x(x)x_\varepsilon + \left(-s + cp(x)\right)y_\varepsilon.$$

Hence, with $\xi = \eta = \varepsilon = 0$, we get

$$x_{\varepsilon\varepsilon}' = H\left(\phi_0(t),K_0\right)x_{\varepsilon\varepsilon} - p\left(\phi_0(t)\right)y_{\varepsilon\varepsilon} + \left[H_x\left(\phi_0(t),K_0\right)x_\varepsilon + H_K\left(\phi_0(t),K_0\right)\kappa(t) +\right.$$

$$+ g_K(\phi_0(t),K_0)\kappa(t) + \phi_0(t)g_{xK}(\phi_0(t),K_0)\kappa(t) - p_x(\phi_0(t))y_\varepsilon]x_\varepsilon +$$
$$+ \phi_0(t)g_{KK}(\phi_0(t),K_0)\kappa^2(t)$$

$$y'_{\varepsilon\varepsilon} = c\psi_0(t)p_x(\phi_0(t))x_{\varepsilon\varepsilon} + [-s+cp(\phi_0(t))]y_{\varepsilon\varepsilon} + c\psi_0(t)p_{xx}(\phi_0(t))x_\varepsilon^2 + 2cp_x(\phi_0(t))x_\varepsilon y_\varepsilon$$

$$x_{\varepsilon\varepsilon}(0) = y_{\varepsilon\varepsilon}(0) = 0,$$

from which we obtain, in the usual way

$$(3.24)\quad \begin{bmatrix} F_{\varepsilon\varepsilon}(0,0,0) \\ G_{\varepsilon\varepsilon}(0,0,0) \end{bmatrix} = \Phi(\omega)\int_0^\omega \Phi^{-1}(t)\cdot$$

$$\cdot \begin{bmatrix} [H_x(\phi_0(t),K_0)x_\varepsilon + H_K(\phi_0(t),K_0)\kappa(t) + g_K(\phi_0(t),K_0)\kappa(t) + \phi_0(t)g_{xK}(\phi_0(t),K_0)\kappa(t) - \\ \qquad - p_x(\phi_0(t))y_\varepsilon]x_\varepsilon + \phi_0(t)g_{KK}(\phi_0(t),K_0)\kappa^2(t) \\ c\psi_0(t)p_{xx}(\phi_0(t))x_\varepsilon^2 + 2cp_x(\phi_0(t))x_\varepsilon y_\varepsilon \end{bmatrix}$$

with x_ε, y_ε given by (3.10).

From (3.9) we obtain

$$(3.25)\quad G_{\xi\xi}(0,0,0)\xi_\eta^2(0,0) + 2G_{\xi\eta}(0,0,0)\xi_\eta(0,0) + G_{\eta\eta}(0,0,0) + G_\xi(0,0,0)\xi_{\eta\eta}(0,0) = 0$$

$$(3.26)\quad G_{\xi\xi}(0,0,0)\xi_\eta(0,0)\xi_\varepsilon(0,0) + G_{\xi\eta}(0,0,0)\xi_\varepsilon(0,0) + G_{\xi\varepsilon}(0,0,0)\xi_\eta(0,0) +$$
$$+ G_{\eta\varepsilon}(0,0,0) + G_\xi(0,0,0)\xi_{\eta\varepsilon}(0,0) = 0$$

$$(3.27)\quad G_{\xi\xi}(0,0,0)\xi_\varepsilon^2(0,0) + 2G_{\xi\varepsilon}(0,0,0)\xi_\varepsilon(0,0) + G_{\varepsilon\varepsilon}(0,0,0) + G_\xi(0,0,0)\xi_{\varepsilon\varepsilon}(0,0) = 0$$

Since we know $G_{\xi\xi}$, $G_{\xi\eta}$, $G_{\eta\eta}$ (from (3.17), (3.18), (3.21)) we can solve (3.25) to find $\xi_{\eta\eta}$ (since $G_\xi(0,0,0) \neq 0$, by assumption).

Similarly, using the values of $G_{\xi\varepsilon}$, $G_{\eta\varepsilon}$, $G_{\varepsilon\varepsilon}$ given by (3.19), (3.22), (3.24), we obtain $\xi_{\eta\varepsilon}$, $\xi_{\varepsilon\varepsilon}$ from (3.26), (3.27). We also have, from (3.17), (3.18), (3.19), (3.21), (3.22), (3.24), the second derivatives of $F(0,0,0)$, and so we can use (3.13)-(3.15) to compute $D_{\eta\eta}(0,0)$,

$D_{\eta\varepsilon}(0,0)$, $D_{\varepsilon\varepsilon}(0,0)$. As pointed out above, once we have these second partial derivatives of D, we can apply critical cases II and III of the Implicit Function Theorem (see [4]) in order to obtain both ξ and η as functions of ε; in this way we would have then solved $F(\xi,\eta,\varepsilon) = 0$. This, together with (3.8), ensures that we have a periodic solution to problem (3.1).

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